SPATIAL AND TEMPORAL PATTERNS OF EPIBENTHIC COMMUNITY AND FOOD WEB STRUCTURES IN THE CHUKCHI SEA BETWEEN 2004 – 2012

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A

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Abstract

The Chukchi Sea shelf, an area undergoing rapid environmental change and concurrently increasing human activity, supports communities of epibenthic organisms and food webs that are sustained by high primary productivity in the overlying water column and are influenced by physical environmental conditions. The goal of this study was to characterize these epibenthic communities (using trawl hauls) and benthic food webs (using carbon and nitrogen stables isotopes) in 2009 and 2012 and to identify persisting or changing patterns between 2004, 2009 and 2012 as part of NOAA's Russian-American Long-term Census of the Arctic (RUSALCA) program. Fifteen stations each were sampled in August to September of 2009 and 2012 in the Chukchi Sea, of which eight repeat stations in the southern Chukchi were sampled in 2004, 2009 and 2012 for temporal comparisons. Epibenthic communities differed in structure between the northern and the southern study regions, with somewhat variable subgroupings within each of those larger regions between years. Overall biomass (mean 49680 ± 45510 g wet weight 1000 m^{-2}) was dominated by echinoderms in particular at northern stations, followed by crustaceans. Repeat stations retained relatively consistent epibenthic community composition across sampling years, despite the at times drastic temporal variability in abundance and biomass. Point in time measurements of water column environmental variables (e.g., salinity, oxygen, temperature) were less strongly correlated to the epifaunal community structure than comparatively stable environmental measures (e.g., substrate type, depth, latitude). Benthic food web structure in the southern Chukchi Sea varied significantly and consistently between water masses in all study years, while $\delta^{15}N$ and $\delta^{13}C$ of pelagic particulate organic matter (PPOM) did not. This indicates that benthic consumers integrate the highly variable POM isotopic signatures and reflect long-term conditions. A persistent gap in $\delta^{15}N$ values between PPOM and epibenthic consumers in nutrient-poor Alaska Coastal Water indicated that the majority of consumers in that water mass did not directly consume POM, which may undergo an additional trophic step of microbial processing before entering the benthic food web. In contrast, shorter food webs without this gap in the nutrient-rich Bering Sea Anadyr Water reflected tight pelagic-benthic coupling. The mostly consistent temporal patterns in epibenthic and food web structure compared to variable standing stock stress the importance of selecting multiple metrics for ecosystem monitoring. The data from this study may serve as a benchmark by which to measure a biological response to climate change and human impacts.

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I could not have completed this work without the guidance of my advisory committee. I would like to thank Seth Danielson for his insight and for offering an oceanographer's perspective to this ignorant biologist. I don't know if I'll ever be able to adequately express my gratitude to my co-advisors Bodil Bluhm and Katrin Iken. I am immensely grateful for the opportunity and the experiences I have been given. I was considerably fortunate to have benefited from their vast expertise, kindness and support. I could not have asked for better mentors.

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1. Introduction

The Chukchi Sea shelf is considered a benthic dominated system (e.g., Feder et al. 2005, Bluhm et al. 2009, Ravelo et al. 2014) due to the large biomass of infaunal and epibenthic organisms (Grebmeier et al. 2006) supported by high pelagic primary productivity, much of which is exported directly to the sea floor. High annual primary productivity occurs seasonally between May and June on the Chukchi Sea shelf. A large portion of the early primary production escapes pelagic grazing, mostly due to low pelagic grazer biomass at the time of the bloom (Campbell et al. 2009). Phytodetritus is then exported to the benthos, providing a food source to the benthic community. Planktonic grazing accounts on average for only 44% of the fate of primary production in the Chukchi Sea (Campbell et al. 2009, Sherr et al. 2009), leaving more than half the primary production available to the benthos. The resulting benthic biomass plays an important role in carbon remineralization (Ambrose et al. 2001), sediment bioturbation (Clough et al. 1997), and as a food source for higher trophic level organisms, such as marine mammals (Ray et al. 2006) and diving birds (Lovvorn et al. 2003).

As typical for many Arctic shelf systems, the epibenthic community of the Chukchi Sea is dominated by echinoderms, arthropods and mollusks. Echinoderms are widespread and ophiuroids comprise a large portion of their biomass in the Chukchi Sea, particularly in the northern regions of the shelf (Piepenburg 2003, Feder et al. 2005, Bluhm et al. 2009, Ravelo et al. 2014). The presence and relative distribution of epibenthic organisms is influenced by a combination of biological interactions and environmental drivers (Feder et al. 2005, Bluhm et al. 2009, Blanchard et al. 2013, Petryashov et al. 2013). For example, the relative dominance of echinoderms and arthropods reverses along a latitudinal gradient, with larger proportions of arthropod biomass in the southern Chukchi Sea giving way to echinoderms poleward (Feder et al. 2005). The dominant snow crab, *Chionoecetes opilio* is the major contributor to the arthropod biomass, but temperature-mediated constraints limit its populations in the colder waters on the northern Chukchi Sea shelf (Foyle et al. 1989, Bluhm et al. 2009). Echinoderms, in turn, are relieved from competitive and predation pressures in the absence of large crabs and flourish in these northern regions (Feder et al. 2005).

Water mass characteristics also influence epibenthic community composition on the Chukchi shelf (e.g., Grebmeier et al. 2006). Water entering the Chukchi Sea via the Bering Strait is comprised of three main water masses, Anadyr Water (AW), Bering Shelf Water (BSW) and Alaskan Coastal Water (ACW), which differ in their hydrographic characteristics and nutrient regimes (Coachman et al. 1975, Walsh et al. 1989). The AW and BSW, which comprise the majority of the flow through Bering Strait, support a higher

benthic biomass than the ACW due to a higher concentration of macronutrients that fuel high levels of primary production (Grebmeier et al. 2006). Community composition can also be variable within the same water mass, based on variations in flow regime in what is an otherwise hydrographically contiguous region (Blanchard et al. 2013). These complex biological and physical interactions and relationships shape epibenthic community structure in the Chukchi Sea.

Physical and biological differences between water masses also influence benthic food web structure in the Chukchi Sea. Besides the different productivity regimes, with higher rates of primary production occurring in the AW and BSW than in the ACW (Walsh et al. 1989, Hansell et al. 1993, Springer & McRoy 1993), river outflow can affect the type and quality of organic matter available to benthic consumers. The Yukon and other smaller rivers introduce seasonally variable amounts of terrestrial organic material into the continental shelf coastal zone (Striegl et al. 2007). As a result, water masses differ in the quantity and quality of the organic carbon available as the basal food source. In the southern Chukchi Sea, particulate organic matter in the ACW along the Alaskan coast likely contains a larger proportion of terrestrial material than the central water masses (Striegl et al. 2007, Iken et al. 2010). Organic material derived from terrestrial plants is less labile than marine primary production, and thus are presumably less suitable as a food source for many aquatic invertebrates (Kristensen 1972, Benner et al. 1986). As such, variations in food sources can impact trophic structure and dynamics of energy flow in benthic communities.

Over the long term, benthic communities and food webs respond to temporal variation in environmental conditions. The Chukchi Sea is seasonally ice-covered, with the supply of fresh phytodetritus to the benthos strongly tied to the timing of the ice retreat and subsequent phytoplankton bloom (Wang et al. 2005). This linkage results in seasonally and interannually variable pulses in food supply available to epibenthic communities that influences benthic food web structure. The hydrographic characteristics of the Chukchi Sea also are seasonally and annually variable, with water advected from the Bering Sea undergoing modification as it travels over the Chukchi Shelf before exiting through Barrow and Herald canyons (Pickart et al. 2005, Weingartner et al. 2005). Circulation may be altered by winds (Woodgate et al. 2005, Danielson et al. 2014) and the locations of water masses may temporally vary as a result of atmospheric forcing (Pisareva et al., in review). Despite the high variability in physical parameters, a limited number of temporal comparisons of benthic community composition shows that although bulk abundance and biomass of some taxa may change over time, the general community structure is rather conservative (Feder et al. 2005, Bluhm et al. 2009). The long-lived

nature of many arctic benthic invertebrates allows them to integrate short-term environmental variability (Bluhm et al. 1998, Post 2002, Kapsenberg & Hofmann 2014); however, if conditions change over longer time scales, patterns in both epibenthic communities and benthic food web structure may also change (Billett et al. 2001). The polar oceans are forecast to be strongly affected by ongoing global climate change (Larsen et al. 2014). Already, the Chukchi Sea has experienced record low maximum and minimum sea ice extent in recent years (NSIDC) with ramifications to primary production (Arrigo et al. 2008), which is likely to have consequences through the food web up to, and including, higher trophic levels.

The present study is part of The National Oceanographic and Atmospheric Administration (NOAA) Russian-American Long-term Census of the Arctic (RUSALCA) program centered in the Chukchi Sea. RUSALCA is an international effort aimed at building a time-series of physical and biological data from the northern Bering and Chukchi seas. As such, the objectives of this study are to 1) *Document spatial patterns in epibenthic community composition, abundance and biomass on the Chukchi Sea shelf in 2009 and in 2012.* 2) *Identify environmental drivers influencing epibenthic community structure in the Chukchi Sea in these years.* 3) *Identify temporal consistency of spatial trends in epibenthic community structure and associated environmental drivers between 2004, 2009 and 2012.* 4) *Construct a benthic food web for the southern Chukchi Sea from 2009 and 2012 collections using $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis.* 5) *Identify temporal consistency of spatial trends in food web structure between 2004, 2009 and 2012.*

2. Materials and Methods

The spatial extent of the present study covers 173 °E to 167 °W and from 67 to 73 °N (Figure 1) with bottom depths ranging from 25 to 152 m. Data for this study were collected in August and September in 2009 and 2012; data from 2004 on epibenthic community structure (Bluhm et al. 2009) and food web structure (Iken et al. 2010) have previously been published and are referenced here for the temporal comparison objectives. Fifteen stations were sampled each in 2009 and 2012 (Figure 1). Eight repeat stations in the southern Chukchi were sampled once during each year, including in 2004, and were used for inter-annual comparisons.

2.1. Study region

The Chukchi Sea is a seasonally ice-covered inflow shelf covering an area of 620,000 km^2 with a mean depth of 58 m (Carmack & Wassmann 2006). Pacific Ocean waters enter the Chukchi Sea via the Bering Strait at an annual average rate of about 0.8 Sv (1 Sv equals 1 million cubic meters per second) (Roach et al. 1995, Woodgate et al. 2005). Three water masses are distinguished entering the Chukchi Sea. The western Bering Strait transmits northward the relatively cold, high-salinity (>32.5), nutrient-rich AW, while waters close to the Alaskan coast are characterized by the warmer, lower-salinity (<31.8) ACW. Located between these two, and with intermediate density, BSW (salinity 31.8-32.5) mixes with AW in the Bering and Anadyr straits, north of which these two water masses are often referred to in aggregate as Bering Shelf Anadyr Waters (BSAW) (Coachman et al. 1975, Coachman 1987, Feder et al. 2005, Weingartner et al. 2005, Grebmeier et al. 2006, Weingartner et al. 2013). Along the western margin of the Chukchi Sea, the cold and fresh Siberian Coastal Current (SCC) enters the Chukchi Sea via Long Strait during summer and fall in some years and can mix with the adjacent BSAW if it spreads offshore, although occasionally the SCC can penetrate all the way to Bering Strait (Weingartner et al. 1999). In summer in the northern portion of the study region, nutrient-depleted BSAW flows northward and exits the shelf along the eastern flank of Herald Canyon, while the western side of the canyon is influenced by cold winter water that originates from the region southeast of Wrangel Island, likely formed by polynya activity near the island (Woodgate et al. 2005, Pickart et al. 2010).

2.2. Epibenthic community

Quantitative sampling for epibenthic invertebrates in 2009 and 2012 was conducted using methods also used for sampling in 2004 in the same study region (Bluhm et al. 2009). Briefly, a plumb-staff beam trawl with a 2.26 m opening and a 7 mm mesh net with a 4 mm cod end liner was used in all three sampling

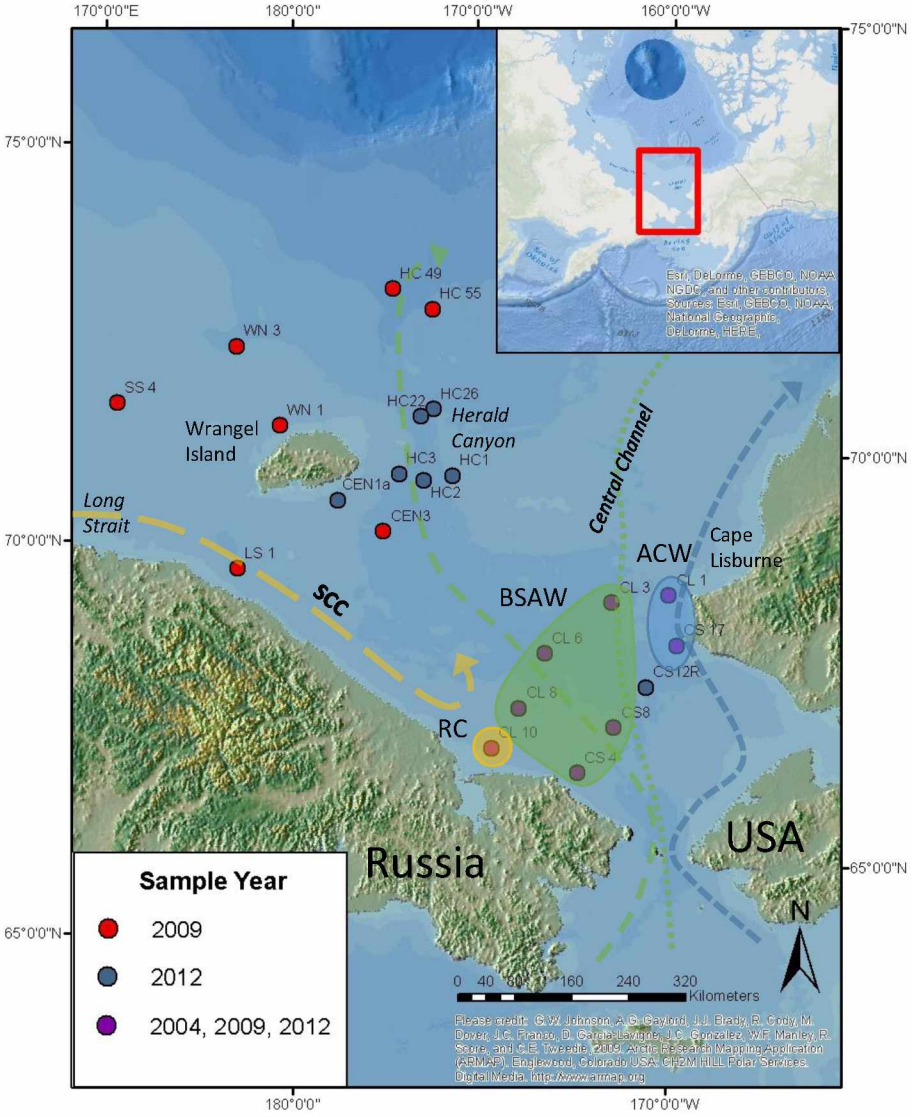

Figure 1. Map of the study area showing sampling stations. Colors denote sampling year. For analysis, stations sampled for stable isotopes were grouped by water masses based on bottom salinity and are indicated by color shaded regions: (ACW) Alaskan Coastal Water, (BSAW) Bering Shelf Anadyr Water, (RC) Russian Coast. Colored arrows indicate main water flow of the ACW (blue) and the two main branches of the BSAW, one through the Central Channel and one through Herald Canyon. Occasionally, the Siberian Coastal Current (SCC) reaches the western Chukchi Sea. (Modified from map provided by Tom Weingartner and Seth Danielson, University of Alaska Fairbanks)

years. In 2009 and 2012, tow duration ranged from 1.5 to 5 min at speeds of ≈1 to 1.5 knots for a trawled area ranging from 135 m^2 to 823 m^2. Trawls were brought on board, washed and sorted to the lowest possible taxonomic level. Large catches were quantitatively subsampled from a well-mixed haul. Organisms were counted and wet weight was acquired at the lowest taxon resolution using spring or digital hanging scales. For colonial organisms (e.g., bryozoans, hydrozoans) only wet weights were recorded. Area trawled was used to estimate abundance and biomass as catch per unit effort (CPUE), which were then normalized to 1000 m^{-2}. Given the semi-quantitative nature of trawl surveys, these data are to be considered gross estimates (Bluhm et al. 2009, Eleftheriou & Moore 2013). Voucher specimens were preserved in 4% seawater-buffered formalin and later transferred to 50% isopropanol for confirmation of field identifications and long-term storage. Taxonomic identifications were conducted by the field teams and later confirmed or corrected with the assistance of taxonomic experts listed in the acknowledgments. Taxonomic names were standardized to the World Register of Marine Species (www.marinespecies.org). Feeding modes of all taxa were identified based on published information (Macdonald 2010, Appeltans et al. 2013) as predators/scavengers, suspension feeders, browsers/grazers, detritivores/deposit feeders, or omnivores in order to spatially and temporally compare community structure based on functional groups.

Hydrographic data (bottom water temperature, salinity, oxygen) were collected at each station from CTD casts (courtesy Dr. R. Pickart, WHOI, available at http://www.whoi.edu/science/po/pickart /newFieldPrograms.htm) and used for hydrographic context for the community analysis. Sediment and water-column chlorophyll, sediment organic content, and infaunal biomass were used as indicators of food availability, and sediment grain size was used as a structural habitat descriptor (data courtesy Drs. J. Grebmeier and L. Cooper, University of Maryland). Infaunal biomass and sediment organic content were only available for 2009.

2.3. Food web structure

Samples for stable isotope analysis were collected and prepared following the methods outlined in Iken et al. (2010) for samples from the 2004 RUSALCA cruise. Food web structure was only determined for eight stations in the southern Chukchi Sea, which were repeatedly sampled every sampling year (Figure 1). Pelagic particulate organic matter (PPOM) was collected at each station from the chlorophyll maximum layer or at 20 m when no chlorophyll maximum layer was present. Three water samples were taken at each station, one each from three different Niskin bottles attached to a CTD rosette. Between 100 and 400 ml of water, depending on PPOM concentration judged by the coloration on the filter, were

filtered onto a pre-combusted GF/F filter (Whatman, 25 mm, nominal retention size 0.7 µm). Surface sediment scrapes were collected at each station (n=3) from an undisturbed van Veen grab (0.1 m^2) to a depth of ≈ 1 cm and stored in Whirl-Pak® plastic bags at -20°C for subsequent stable isotope analysis of sediment particulate organic matter (SPOM). After SPOM samples were collected, remaining grab sediments were sieved over 1 mm mesh and three to five specimens each of representative infaunal taxa collected. Three to five replicate individuals from the most common epibenthic invertebrates and fishes were collected from the plumb-staff beam trawl described above. Specific care was taken to collect taxa that had also been collected in 2004 to facilitate a temporal comparison across all three project years. Replicate individuals were sub-sampled for muscle or body wall to target slow turn-over tissues (Lorrain et al. 2002). When sufficient mass could not be obtained from tissue samples, whole organisms were taken, though guts were removed where practical. Samples were frozen at -20°C prior to drying at 60°C for 24 h and then stored for later analysis.

Samples containing carbonate were treated using 1N HCl prior to analysis. Organisms and sediments were treated until bubbling ceased; the HCl was then removed and the sample was re-dried at 60°C for 24 h. Sediment samples were rinsed with de-ionized water after HCl treatment until pH returned to neutral before drying. All samples were freeze dried before being analyzed. PPOM filters were treated by fuming in HCl vapors for 24 h and then re-dried at 60°C for 24 h. Because lipids are isotopically depleted and can confound interpretation of trophic position (Post 2002, Sweeting et al. 2006), lipids were removed from all 2009 and 2012 samples using 2:1 chloroform-methanol. Lipids had not been removed from the 2004 samples (Iken et al. 2010), making it necessary to correct those data for lipid content before conducting temporal comparisons with the data from 2009 and 2012. A sub-set of the 2009 samples covering the most common taxa were analyzed both before and after lipid extraction. The average difference in $\delta^{13}C$ values was determined for each taxon and the difference was applied to the matching taxon in the 2004 dataset to correct those data for lipid content. I decided against using the method of an arithmetic correction for lipid content based on an organism's C:N ratio (McConnaughey & McRoy 1979) because there often is no clear relationship between C:N ratio and the differences between lipid-extracted and non-treated $\delta^{13}C$ values in polar invertebrates (Kiljunen et al. 2006, Sweeting et al. 2006).

Stable isotope samples were measured at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks on a Thermo Finnigan Delta Isotope Ratio Mass Spectrometer (IRMS) with Vienna Pee Dee

Belemnite and atmospheric nitrogen as carbon and nitrogen standards, respectively. Isotopic ratios were expressed in standard δ notation as parts per thousand (‰) using the equation:

$$\delta X=[(R_{sample}/R_{standard}) - 1] \cdot 1000$$

where X is the ^{13}C or ^{15}N of the sample and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

2.4. Data analysis

Epibenthic community structure was analyzed separately for 2009 and 2012 using the multivariate statistics software package PRIMER v6 (Clarke & Gorley 2006). A Bray-Curtis similarity matrix was created using fourth-root transformed abundance and biomass data to reduce the influence of dominant taxa on the analyses. A hierarchical cluster analysis was used to group stations by similarity (group average) based on the similarity matrix, and a SIMPROF test was run to test the significance of clusters ($\alpha = 0.05$). A similarity of percentages (SIMPER) routine was run to identify the taxa contributing the most (≈ 50%) to similarities within station clusters as well as dissimilarities among clusters. Diversity indices (Shannon's diversity, Pielou's evenness) were calculated from abundance data using the DIVERSE routine. Diversity measures, as well as total abundance and biomass, were compared among study regions within each sampling year using ANOVA (SYSTAT13). Data were tested for normal distribution and homogeneity of variances using Shapiro-Wilks and Bartlett's tests respectively. Data were transformed (log) in order to meet the assumptions of ANOVA whenever appropriate. For these analyses, stations within a year were often grouped into a northern and southern station group (see Table 1).

Environmental variables were normalized to a common measurement scale in PRIMER v6 and then correlated with the biological matrix based on biomass (fourth-root transformed) for each year using the BIO-ENV suite. In addition to multivariate analysis, Spearman rank correlations were used to identify relationships between individual environmental variables and bulk abundance or biomass, as well as the abundance or biomass of dominant phyla (SYSTAT v13).

Temporal comparisons of epibenthic community were conducted using data from the eight repeat stations in the southern Chukchi Sea in 2004, 2009 and 2012 (Figure 1). Because epibenthic fauna were identified to different taxonomic levels in different years, all species lists were collapsed to the lowest common taxonomic level found across all study years, and environmental variables were reduced to those available for all three study years (latitude, substrate category, bottom temperature/salinity/oxygen, water-column chlorophyll, water depth). Substrate category was

Table 1. Station table for RUSALCA 2004 (repeat stations only), 2009, and 2012 cruises. Stations are listed by sampling date. RUSALCA 2004 stations are listed with original *R* designation, as well as corresponding *C* station identification used in later years. Stations sampled in 2009 and 2012 are divided into northern (N) and southern (S) regions. Underlined numbers indicate minimum and maximum values for each year.

	Station	Date	Latitude °N	Longitude °W	Depth (m)	Abundance (ind. 1000 m^{-2})	Biomass (g ww 1000 m^{-2})	Number of taxa	Pielou's evenness *J'*	Shannon Diversity *H'*(log_e)	Substrate Category	Bottom Temp (C°)	Salinity	Oxygen (ml l^{-1})
	2004													
	R11/CS4	11-Aug-04	66.93	-170.99	43	15437	16644	28	0.48	1.61	Soft	1.7	33.2	6.2
	R13/CS8	11-Aug-04	67.43	-169.64	51	9712	30478	22	0.57	1.77	Soft	2.5	32.9	5.1
	R17/CS17	12-Aug-04	68.32	-167.07	38	1828	17027	46	0.77	2.93	Hard	7.0	31.0	6.6
	R18/CL1	13-Aug-04	68.98	-166.89	46	6133	60249	20	0.35	1.06	Hard	7.9	31.3	6.7
	R20/CL3	13-Aug-04	69.00	-168.86	54	16594	64475	22	0.25	0.77	Soft	3.7	32.3	7.2
	R23/CL6	14-Aug-04	68.51	-171.46	56	11605	7821	17	0.78	2.20	Soft	2.2	32.9	5.3
	R25/CL8	15-Aug-04	67.86	-172.57	49	10848	9693	20	0.82	2.45	Soft	1.7	33.0	5.2
	R27/CL10	15-Aug-04	67.41	-173.64	34	2858	1628	21	0.69	2.11	Hard	-1.5	32.9	5.5
	2009													
N	LS1	8-Sep-09	69.83	178.01	44	24945	**206180**	25	0.38	1.21	Soft	3.7	**25.8**	7.4
N	SS4	9-Sep-09	71.82	172.99	42	24712	35518	19	0.38	1.13	Hard	-1.5	31.5	5.9
N	WN3	10-Sep-09	72.66	177.67	74	40663	83632	26	0.56	1.81	Soft	-1.5	32.8	**2.0**
N	WN1	11-Sep-09	71.66	179.50	33	31216	123456	29	0.76	2.57	Soft	**-0.4**	30.5	7.0
N	HC49	13-Sep-09	73.36	-175.62	152	**35441**	83425	**10**	**0.27**	**0.62**	Soft	-0.1	34.5	3.4
N	HC55	14-Sep-09	73.06	-174.01	94	20243	52026	15	0.37	0.99	Soft	-1.0	33.0	5.9
N	CEN3	6-Sep-09	70.28	-176.67	58	5660	55719	16	0.47	1.29	Soft	-1.6	33.2	5.5
S	CS8	4-Sep-09	67.43	-169.61	51	8663	95043	19	0.60	1.77	Soft	1.8	32.7	3.7
S	CL1	24-Sep-09	68.95	-166.92	49	4824	28794	21	0.69	2.12	Soft	3.2	32.0	6.3
S	CL3	24-Sep-09	69.00	-168.90	56	**782**	24966	14	0.66	1.74	Soft	2.3	32.2	5.0
S	CL6	25-Sep-09	68.52	-171.46	57	9870	117004	12	0.54	1.34	Soft	1.8	32.8	3.1
S	CL8	25-Sep-09	67.87	-172.55	50	33295	96470	15	0.67	1.82	Soft	-0.1	**33.0**	3.2
S	CS4	26-Sep-09	66.93	-170.99	45	8709	47544	17	0.53	1.50	Soft	**3.9**	31.4	6.9
S	CL10	26-Sep-09	67.40	-173.60	38	5765	**13349**	**27**	0.50	1.66	Hard	3.7	28.7	**7.4**
S	CS17	27-Sep-09	68.30	-167.04	40	2110	46565	23	**0.82**	**2.58**	Hard	3.8	31.9	5.5
	2012													
N	CEN1a	6-Sep-12	70.67	-178.41	40	**421**	**2801**	25	0.54	1.73	Hard	-0.9	29.3	5.4
N	HC1	7-Sep-12	70.97	-173.98	52	727	5713	17	0.61	1.74	Hard	0.4	33.5	5.7
N	HC2	7-Sep-12	70.90	-175.00	70	2527	22551	**8**	**0.15**	0.31	Soft	-1.6	**33.6**	5.2
N	HC3	7-Sep-12	71.03	-175.99	50	11103	15976	34	0.41	1.45	Soft	**-1.8**	33.4	5.4
N	HC26	8-Sep-12	71.79	-174.35	57	8640	58623	17	**0.15**	**0.43**	Soft	**-1.8**	32.9	6.2
N	HC22	8-Sep-12	71.71	-174.91	73	2008	22819	25	0.43	1.39	Soft	-1.1	33.3	5.8
S	CS4	30-Aug-12	66.93	-170.88	45	6180	24636	34	**0.75**	**2.65**	Soft	1.4	32.4	6.3
S	CS17	1-Sep-12	68.34	-167.09	40	2715	10915	**49**	0.46	1.80	Hard	**6.5**	**30.8**	6.9
S	CL1	1-Sep-12	68.96	-166.99	50	1475	5593	29	0.54	1.80	Soft	3.2	32.2	**7.2**
S	CL6	2-Sep-12	68.51	-171.56	57	13314	11419	23	0.66	2.07	Soft	1.4	32.8	4.2
S	CL3	12-Sep-12	69.02	-168.84	54	1664	13729	29	0.68	2.29	Soft	1.0	32.6	5.6
S	CL8	13-Sep-12	67.87	-172.61	50	20104	27256	26	0.68	2.23	Soft	1.1	32.9	4.3
S	CL10	13-Sep-12	67.40	-173.61	34	14796	11875	25	0.52	1.68	Hard	-1.2	32.7	5.1
S	CS8	14-Sep-12	67.43	-169.61	52	29230	48312	43	0.68	2.57	Soft	-0.8	33.3	**3.8**
S	CS12	15-Sep-12	67.86	-168.27	58	**36715**	**103876**	30	0.51	1.72	Soft	-0.2	33.1	3.9

determined as either hard or soft substrate based on field observations and sediment grain size data. The environmental variables depth and salinity were then removed from the matrix because of their correlation (≥ 95%) to other environmental variables (salinity to substrate category, temperature, oxygen, and depth; depth to latitude, substrate category, and salinity). Cluster analysis was used to

identify groups of stations based on environmental conditions across years and those were then visualized in non-metric multidimensional scaling (nMDS) plots. Analysis of similarity (ANOSIM) was used to test similarity of community structure among years. A SIMPER routine determined if the most influential taxa remained the same throughout the three study years and measures of diversity were compared across years (ANOVA). Results from the BIO-ENV analysis were used to determine whether environmental variables displayed the same relationships to the biological matrices among years.

Trophic analyses were done on stations sampled in all three study years in the southern Chukchi Sea. Repeat stations were assigned to water masses based on bottom water salinity; stations with salinity below 31.8 were assigned to ACW, while those above 31.8 were assigned to BSAW (Coachman et al. 1975). Station CL10 (in 2004 referred to as R27) can be influenced by BSAW, periodically the Siberian Coastal current, and the freshwater outflow from the Kolyuchin Lagoon. The resulting variable salinity signal (Table 1) resulted in its separate designation as Russian Coast (RC) station. Trophic level of consumers for food web analysis was calculated with the equation:

$$\text{Trophic level} = (\delta^{15}N_{consumer} - \delta^{15}N_{PPOM})/3.4 + 1$$

where 3.4 is the assumed enrichment in $\delta^{15}N$ between trophic levels (Vander Zanden & Rasmussen 2001) and the $\delta^{15}N$ value of PPOM is used as the baseline for calculating trophic levels of consumers. For each sampling year, food web structure was determined from trophic level distribution and food web length was determined as the difference between the minimum and maximum trophic levels per water mass (Figure 1). Consumer taxa were matched up with the epibenthic community trawl data to appraise the relative biomass contribution to different trophic levels among water masses. Where stable isotope data were not available, the biomass contributions were classified as “unknown” trophic level. Temporal comparisons of trophic levels and food web length were conducted by only using the same taxa that were collected in each year. ANOVA was used to compare $\delta^{13}C$ and $\delta^{15}N$ values of POM and of select organisms among water masses and among the three years using SYSTAT v13.

3. **Results**

3.1 Epibenthic community structure

3.1.1 Epibenthic community structure in 2009

Across all 15 stations sampled in 2009, 98 epibenthic taxa from 9 phyla were identified. Of these taxa, 81 were identified to genus level or lower. The majority of all taxa were mollusks (26 taxa), arthropods (22 taxa), and echinoderms (22 taxa) (Appendix 1). Patterns in diversity (H') were variable, with no distinct pattern emerging and no significant difference between northern and southern (ANOVA, $p = 0.12$) station groups (Table 1). Feeding types of the 98 taxa included 49 predators/scavengers, which comprised 40 to 82% of the number of taxa at every station. Twelve taxa were classified as suspension feeders, six as deposit feeders/detritivores, five as omnivores, four as browsers/grazers, and the remaining 22 taxa were classified as "other" because of insufficient taxonomic resolution or unknown feeding habits (Appendix 1).

Total epifaunal abundance in 2009 was higher at northern than southern stations (Figure 2A, ANOVA $p = 0.01$, mean at northern stations 26,126 ± 10,562 ind. 1000 m^{-2} versus 9,252 ± 9,576 ind. 1000 m^{-2} at southern stations), largely because of the considerable number of echinoderms, especially ophiuroids. Total abundance across the entire study region was, on average, dominated by echinoderms (mean abundance = 8,286 ± 10,393 ind. 1000 m^{-2}), which comprised 48% of total abundance (Figure 3A.) Arthropods contributed on average 21% (mean = 3,621 ± 4,018 ind. 1000 m^{-2}) to total abundance. The brittle star *Ophiura sarsii* was the most numerous single taxon across the study region, occurring at 8 of the 15 stations and making up 17% (mean = 2,900 ± 5,805 ind. 1000 m^{-2}) of total abundance. The snow crab, *Chionoecetes opilio*, and the moon snail, *Cryptonatica affinis*, were the most regularly occurring species, being present at 14 and 11 of 15 stations, respectively. Predators/scavengers were the most abundant feeding guild (mean 8,780 ± 8,989 ind. 1000 m^{-2}), comprising 53% of the total abundance, and deposit/detritus feeders were the second-most abundant group (27%; mean 4,487 ± 6,729 ind. 1000 m^{-2}).

Biomass in 2009 was relatively evenly distributed between the northern and southern study regions (Figure 2B, ANOVA $p=0.3$). Biomass was dominated by echinoderms (46% of total biomass, mean 33,767 ± 51,881 g wet weight 1000 m^{-2}) and arthropods (34%, mean 24,904 ± 22,748 g wet weight 1000 m^{-2}).

Mollusks contributed 13% of total biomass (mean 9,319 ± 9,654 g wet weight 1000 m^{-2}). The brittle star *O. sarsii* and the snow crab *C. opilio* dominated the total biomass with a combined 47%. Echinoderms

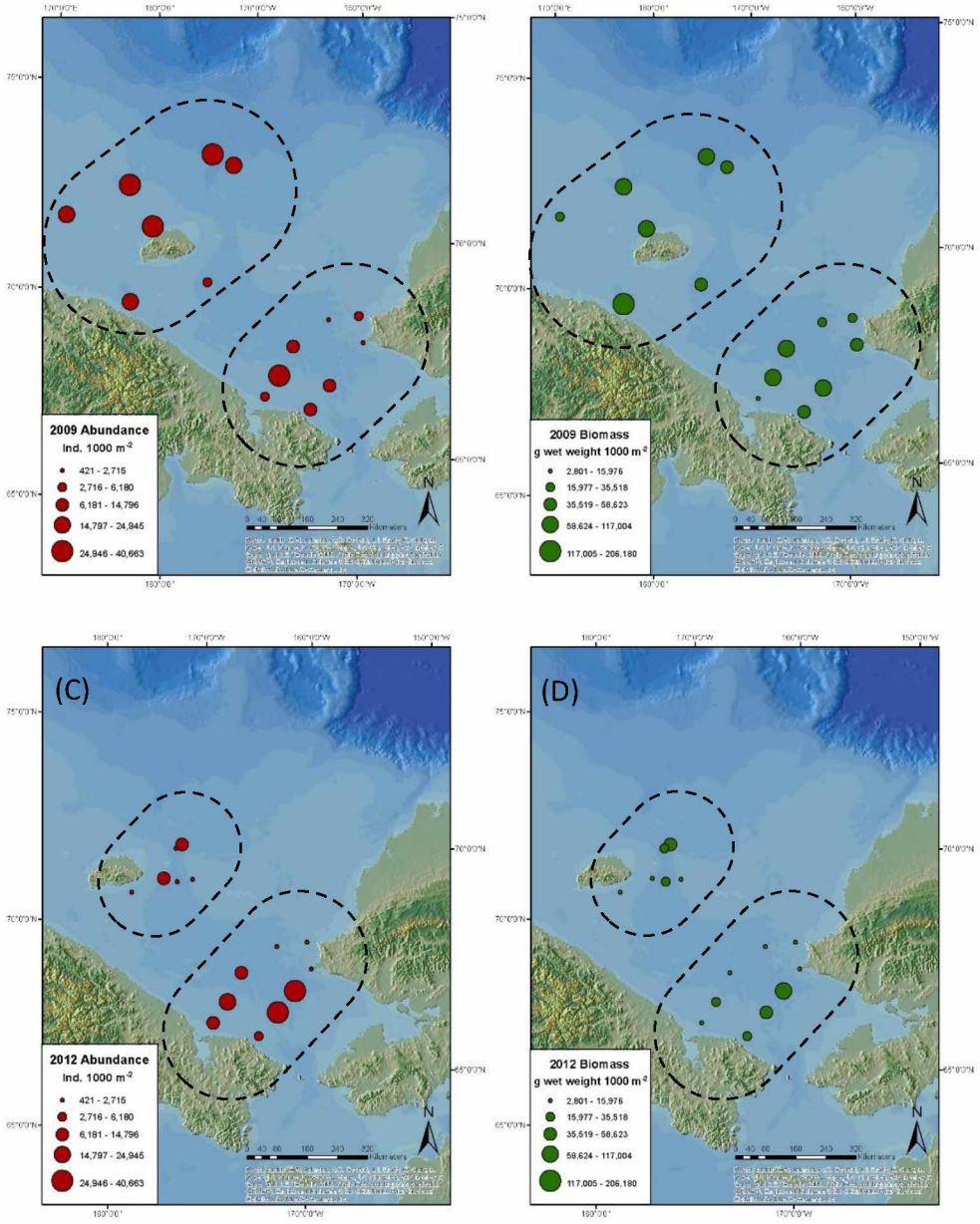

Figure 2. Epifaunal abundance and biomass at stations sampled during RUSALCA 2009 (A-B) and 2012 (C-D). Circle size depicts bins delineated by Jenk's natural breaks created using ArcMap 10.2. Dashed outlines depict northern/southern station groupings.

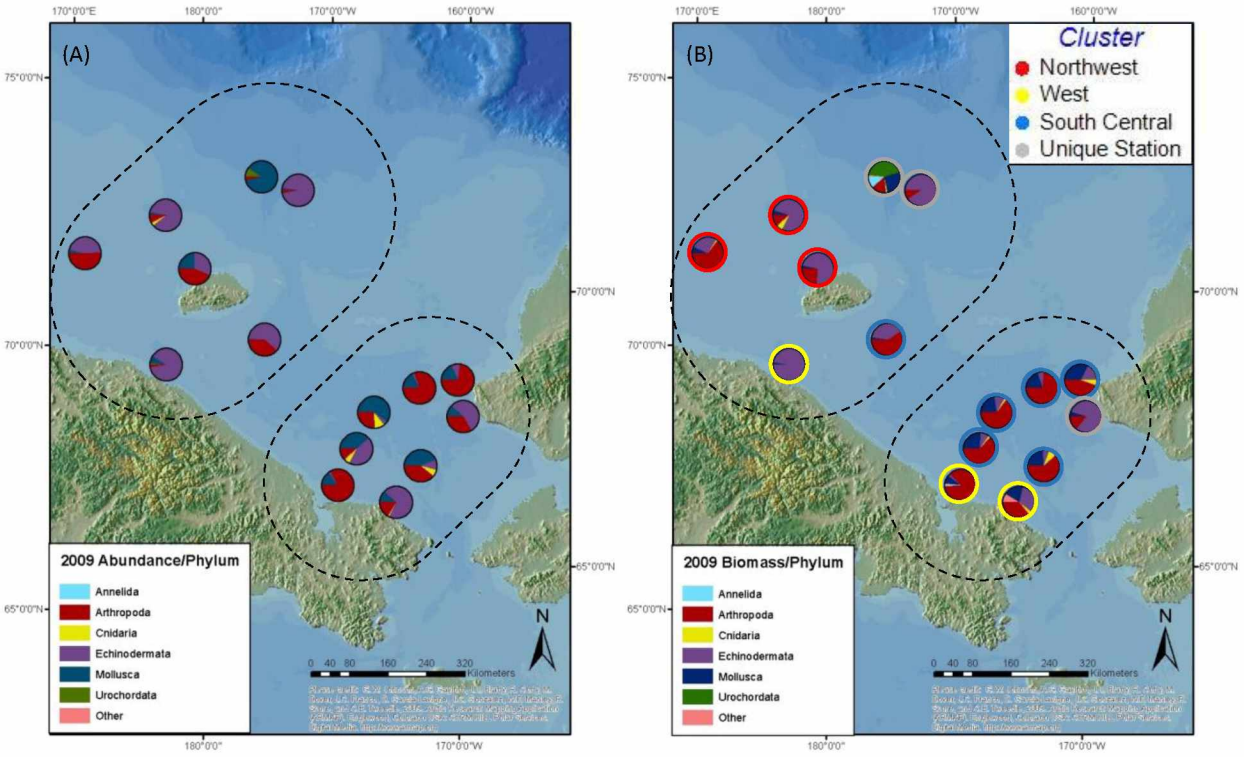

Figure 3. Relative contribution by phylum to epibenthic (A) abundance and (B) biomass per station sampled in 2009. Colored rings around pie charts in Figure 3B denote station clusters identified by hierarchal clustering (group average, 4th-root transformed biomass, Bray-Curtis similarity, see Figure 4). Dashed outlines depict northern/southern station groupings.

made the largest contribution to the biomass at northern stations (67%), whereas they only contributed 18% of the biomass at southern stations. The majority of the biomass at southern stations was contributed by arthropods (56%) and mollusks (22%). Some groups were overall minor biomass contributors but dominated at single stations, such as ascidians (Urochordata), which contributed 43% of the total biomass at station HC46 in northern Herald Canyon (Figure 1, 3B). As with abundance, predators/scavengers made up 68% of the total biomass (mean 48,815 ± 49,411 g wet weight 1000 m^{-2}), while deposit feeders/detritivores were the second-largest feeding guild with 16% of the total biomass (mean 11,579 ± 17,452 g wet weight 1000 m^{-2}).

Three significant station groups were identified at 43% similarity by the cluster analysis based on a biomass-based similarity matrix, and three stations did not cluster with any other group (Figure 4, SIMPROF, p=0.05). Northern and southern stations, respectively, grouped closer with each other than between north and south (Figure 4). Within the northern and southern regions, geographically close stations mostly grouped together, with a northwestern group consisting of three stations north and

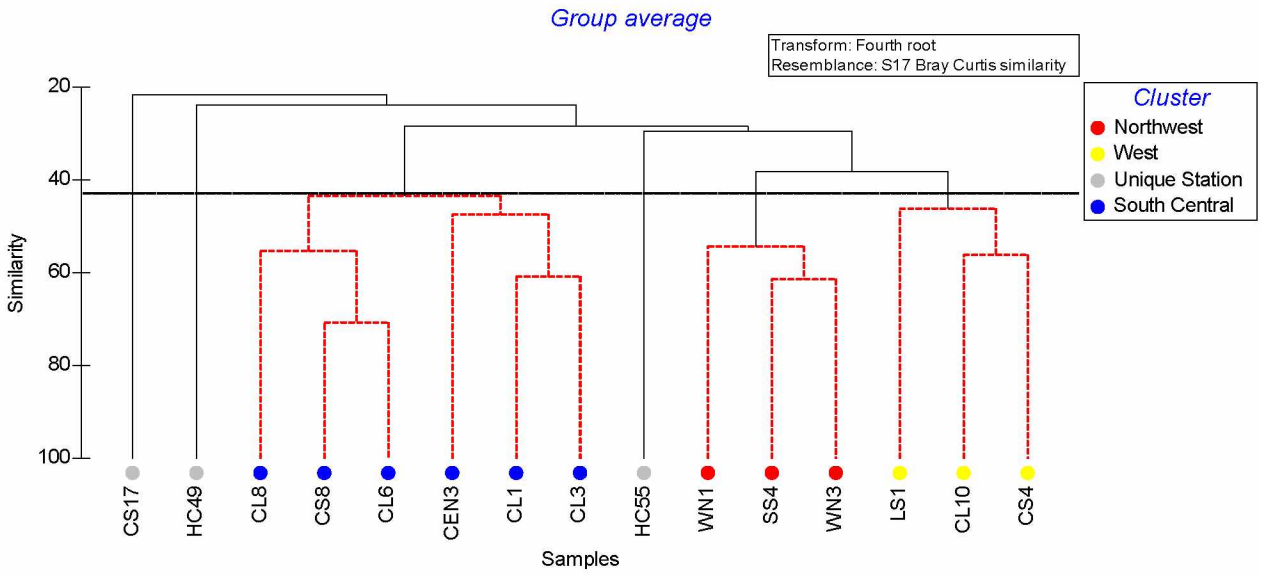

Figure 4. Community similarity identified by hierarchical clustering for stations sampled in 2009. Red dotted lines denote non-significant groups while black lines indicate significant differences among groups (SIMPROF, p=0.05). Grouping is based on 4th-root transformed biomass resemblance (Bray-Curtis) matrix.

west of Wrangel Island, a western coastal group consisting of three stations along the Russian coast from Long Strait to north of Bering Strait, and a central group that encompassed most of the central and southern Chukchi stations (Figure 3B). The average community similarity within station groups ranged from 49% to 57%, with highest similarity within the northwestern group (Table 2). This northwestern group was defined by a large biomass contribution of the isopod *Saduria* spp. and the ophiuroids *O. sarsii* and *O. sericeum*, all together contributing 37% similarity within the group. In the western group, the holothuroid *Myriotrochus rinkii* and whelks of the family Buccinidae contributed 22% to similarity, while the central group was defined by a large contribution of *C. opilio* to group similarity (28%, Table 2). Average dissimilarity between groups ranged from 62% to 78% (Table 3). Three taxa were primarily responsible for the dissimilarity between the three unique stations and the other station groups: Ascidiacea at station HC49, the mud star *Ctenodiscus crispatus* at HC55, and the basket star *Gorgonocephalus* sp. at CS17.

The combination of the fewest environmental variables that had the highest correlation with the biomass-based community resemblance matrix consisted of latitude, water depth, infaunal biomass, and water-column chlorophyll (Spearman rank correlation ρ=0.562, Table 4). Depth, infaunal biomass, and latitude were the most influential factors in these multivariate correlations. For univariate analyses, the

Table 2. Taxa contributing most to similarity ($\approx 50\%$) within groups identified by hierarchical clustering, based on fourth-root transformed biomass data for 2009 and 2012. Contrib.: contribution, Cum.: cumulative.

2009	Av. Biomass (g ww 1000 m^{-2})	Av. Similarity (%)	Similarity SD	Contrib. (%)	Cum. (%)
Group **South Central**					
Average similarity: 48.55%					
Taxa					
Chionoecetes opilio	13.4	13.6	3.8	28.0	28.0
Leptasterias spp.	5.3	4.3	2.4	8.9	36.8
Crangonidae	4.8	4.3	7.4	8.8	45.6
Pagurus rathbuni	5.2	4.2	1.4	8.7	54.4
Group **Northwest**					
Average similarity: 56.75%					
Taxa					
Saduria spp.	11.1	8.2	4.1	14.5	14.5
Ophiura sarsii	10.5	6.7	7.8	11.8	26.3
Ophiocten sericeum	10.3	6.1	4.4	10.7	37.0
Myriotrochus rinkii	5.9	3.9	3.3	6.9	43.9
Sabinea septemcarinata	4.8	3.7	4.9	6.5	50.3
Group **West**					
Average similarity: 49.56%					
Taxa					
Myriotrochus rinkii	8.0	6.0	1.5	12.1	12.1
Buccinidae	6.1	5.0	7.4	10.0	22.2
Hyas coarctatus	5.8	4.6	2.8	9.3	31.5
Chionoecetes opilio	7.1	4.6	1.3	9.2	40.7
Leptasterias spp.	6.1	4.5	2.6	9.0	49.7

2012	Av. Biomass (g ww 1000 m^{-2})	Av. Similarity (%)	Similarity SD	Contrib. (%)	Cum. (%)
Group **South Central**					
Average similarity: 34.75%					
Taxa					
Cryptonatica affinis	9.1	6.2	4.9	17.9	17.9
Leptasterias groenlandica	7.2	4.1	8.4	11.8	29.6
Actiniaria	6.0	3.5	2.4	10.0	39.7
Serripes sp.	5.3	2.5	2.8	7.2	46.8
Chionoecetes opilio	5.2	2.1	1.1	6.0	52.9
Group **East**					
Average similarity: 44.64%					
Taxa					
Chionoecetes opilio	8.5	8.7		19.5	19.5
Argis lar	5.6	6.2		14.0	33.5
Pagurus trigonocheirus	4.3	5.0		11.2	44.6
Neptunea communis	4.0	4.3		9.7	54.3
Group **North 2**					
Average similarity: 43.21%					
Taxa					
Eualus sp.	6.9	11.7		27.1	27.1
Chionoecetes opilio	5.0	7.1		16.3	43.4
Ophiura sarsii	4.3	5.7		13.2	56.5
Group **North 1**					
Average similarity: 50.27%					
Taxa					
Ctenodiscus crispatus	12.8	19.9	4.5	39.7	39.7
Chionoecetes opilio	6.7	10.9	4.2	21.6	61.3
Pagurus capillatus	3.0	4.4	21.4	8.8	70.1

only common predictor for bulk estimates of total abundance and biomass was a positive correlation with percent mud, which was also positively correlated to mollusk biomass. All significant correlations with percent gravel were negative (total, arthropod, and mollusk biomass) (Table 5). Little consistency was found in the relationship of biomass of major taxa with other environmental variables. All significant relationships of abundance measures with indicators of food supply were positive; in contrast, infaunal biomass was not a significantly correlated variable (Table 5).

Table 3. Top three epifaunal taxa contributing most to dissimilarity between groups identified by hierarchical clustering for 2009 and 2012.

Taxa	Average Biomass (g ww 1000 m^{-2})		Av. Dissimilarity	SD of dissimilarity	Contrib. (%)	Cum. (%)
2009						
Groups **Central & West**						
Average dissimilarity = 64.49%	**CEN**	**W**				
Myriotrochus rinkii	0.0	8.0	4.5	2.4	6.9	6.9
Chionoecetes opilio	13.4	7.1	3.6	1.6	5.6	12.5
Cryptonatica affinis	6.2	5.7	3.1	2.6	4.8	17.3
Groups **Central & Northwest**						
Average dissimilarity = 77.55%	**CEN**	**NW**				
Saduria spp.	0.0	11.1	5.5	3.6	7.1	7.1
Chionoecetes opilio	13.4	3.1	5.0	2.5	6.5	13.5
Ophiocten sericeum	0.0	10.3	5.0	3.0	6.4	19.9
Groups **West & Northwest**						
Average dissimilarity = 61.75%	**W**	**NW**				
Saduria spp.	0.0	11.1	5.2	4.0	8.4	8.4
Ophiocten sericeum	0.0	10.3	4.7	3.0	7.6	15.9
Ophiura sarsii	0.0	10.5	4.7	7.5	7.5	23.5
2012						
Groups **South Central & East**						
Average dissimilarity = 78.06%	**SC**	**E**				
Cryptonatica affinis	9.1	1.2	3.6	3.8	4.6	4.6
Leptasterias groenlandica	7.2	0.0	3.2	5.8	4.1	8.7
Actiniaria	6.0	0.0	2.8	2.3	3.6	12.3
Groups **South Central & North 2**						
Average dissimilarity = 79.48%	**SC**	**N2**				
Cryptonatica affinis	9.1	0.8	4.4	4.2	5.6	5.6
Leptasterias groenlandica	7.2	1.0	3.1	3.7	3.9	9.5
Actiniaria	6.0	0.5	3.1	2.0	3.8	13.3
Groups **East & North 2**						
Average dissimilarity = 70.31%	**E**	**N2**				
Eualus sp.	0.0	6.9	5.0	8.5	7.1	7.1
Ophiura sarsii	0.0	4.3	3.1	3.0	4.4	11.6
Neptunea communis	4.0	0.0	2.9	6.9	4.1	15.7
Groups **South Central & North**						
Average dissimilarity = 81.36%	**SC**	**N**				
Ctenodiscus crispatus	0.0	12.8	6.8	3.4	8.3	8.3
Cryptonatica affinis	9.1	2.4	3.5	3.9	4.3	12.6
Leptasterias groenlandica	7.2	0.7	3.2	3.2	4.0	16.6
Groups **East & North**						
Average dissimilarity = 73.66%	**E**	**N**				
Ctenodiscus crispatus	0.0	12.8	9.1	5.1	12.4	12.4
Neptunea ventricosa	4.8	0.0	3.4	2.9	4.6	17.0
Neptunea communis	4.0	0.0	2.8	4.4	3.9	20.9
Groups **North 2 & North**						
Average dissimilarity = 72.91%	**N2**	**N**				
Ctenodiscus crispatus	0.0	12.8	11.7	4.5	16.1	16.1
Eualus sp.	6.9	0.7	5.8	2.8	7.9	24.0
Ophiura sarsii	4.3	0.0	3.9	2.5	5.4	29.4

Table 4. Combination of environmental variables most correlated to epifaunal resemblance matrix based on biomass 2009 and 2012, from 12 and 10 variables used in 2009 and 2012, respectively. Correlation coefficients are in parentheses.

Number of variables	Best combination of variables	Second best combination of variables
	2009	
1	Depth (0.379)	Latitude (0.319)
2	Depth, Infaunal Biomass (0.466)	Latitude, Infaunal Biomass (0.428)
3	Latitude, Depth, Infaunal Biomass (0.537)	Depth, H_2O chlorophyll, Infaunal Biomass (0.513)
4	Latitude, Depth, Infaunal Biomass, H_2O chlorophyll (0.562)	Salinity ,Latitude, Depth, Infaunal Biomass (0.550)
	2012	
1	% Gravel (0.506)	Depth (0.240)
2	Latitude, % Gravel (0.465)	Sediment chlorophyll, % Gravel (0.417)
3	Temperature, Sediment chlorophyll, % Gravel (0.478)	Temperature, Latitude, % Gravel (0.472)
4	Oxygen, Latitude, Depth, % Gravel (0.498)	Temperature, Latitude, Depth, % Gravel (0.493)
5	Temperature, Depth, H_2O chlorophyll, Sediment chlorophyll, % Gravel (0.520)	Temperature, Oxygen, Latitude, Depth, % Gravel (0.504)
6	Temperature, Latitude, Depth, H_2O chlorophyll, Sediment chlorophyll, %Gravel (0.524)	Temperature, Oxygen, Depth, H_2O chlorophyll, Sediment chlorophyll,% Gravel (0.510)

Table 5. Spearman correlation coefficients for environmental variables with bulk abundance and biomass in 2009 and 2012. Values in bold are above the critical value (0.443) for statistical significance ($p < 0.05$).

		2009					2012				
		Total Abundance	Total Biomass	Arthropod Biomass	Echinoderm Biomass	Mollusk Biomass	Total Abundance	Total Biomass	Arthropod Biomass	Echinoderm Biomass	Mollusk Biomass
Hydrography	Temperature	**-0.457**	-0.207	-0.264	-0.164	0.261	-0.105	-0.340	-0.032	-0.422	**0.488**
	Salinity	0.168	0.15	0.282	-0.229	0.218	0.236	**0.425**	0.157	0.400	-0.032
	Oxygen	-0.229	-0.248	-0.391	0.202	**-0.490**	**-0.650**	-0.354	-0.296	-0.036	-0.239
	Latitude	**0.486**	0.157	-0.289	0.257	-0.329	**-0.525**	-0.146	-0.404	0.339	**-0.482**
	Depth	0.218	0.164	0.036	-0.146	0.221	0.218	**0.550**	-0.064	**0.657**	0.375
Sediment	%Gravel	-0.378	**-0.68**	**-0.611**	0.073	**-0.786**	-0.040	-0.379	-0.219	-0.023	**-0.696**
	%Sand	-0.389	-0.30	-0.10	0.307	-0.396	-0.350	-0.389	0.014	-0.421	-0.261
	%Mud	**0.471**	**0.589**	0.257	-0.046	**0.650**	0.275	0.404	-0.086	**0.457**	0.429
Food Supply	Sediment Chlorophyll	0.091	0.331	0.231	**0.518**	0.147	0.439	0.339	0.400	0.029	**0.739**
	H_2O Chlorophyll	-0.413	0.079	**0.665**	-0.220	**0.445**	0.307	0.207	-0.064	0.193	0.146
	Sediment Organic Carbon	0.345	0.374	0.352	-0.136	**0.458**					
	Infaunal Biomass	0.068	0.389	0.314	0.389	0.257					

3.1.2 Epibenthic community structure in 2012

A total of 175 epibenthic taxa were identified in 2012, with 125 at genus level or lower, representing 11 phyla (Table 1). Arthropods were the most species-rich group with 47 taxa, followed by mollusks (42) and cnidarians (20). Northern stations were variable in taxon richness despite their geographic vicinity (Table 1). Southern stations generally had higher diversity indices than northern stations (*H'*= 2.09 (± 0.35) and 1.17 (± 0.58), *J'* = 0.61 (± 0.10) and 0.38 (± 0.18), respectively; ANOVA, p=0.004 and p=0.01, respectively). As in 2009, predators/scavengers were the most species-rich functional group (81 taxa), followed by suspension feeders (49 taxa). Seven taxa each represented browsers/grazers and omnivores, while 10 taxa were classified as deposit feeders/detritivores.

Abundance in 2012 ranged from 421 ind. 1000 m^{-2} in the region southeast of Wrangel Island to 36,715 ind. 1000 m^{-2} in the southern Chukchi Sea (mean 10,108 ± 10,739 ind. 1000 m^{-2}, Table 1, Figure 2C) but unlike 2009, abundance did not differ between north and south regions (ANOVA p=0.08). Arthropods dominated the overall abundance (57%) across the entire study region (Figure 5A). The high proportion of arthropods was partially due to high abundances of the snow crab, *C. opilio*, which alone comprised over 19% of the total abundance. At the northern stations, arthropods and echinoderms each contributed 48% of the total abundance, while southern stations were dominated by only arthropods (56%) (Figure 5A). The most regularly occurring species across the entire study region were snow crab *C. opilio* (13 stations), *C. affinis* (11 stations), and the hermit crab *Pagurus capillatus* (11 stations). Predator/scavengers were the most abundant feeding guild, comprising 77% of the total abundance. This guild was dominant at all but three stations (HC2, HC22, HC26) in the Herald Canyon region, where the deposit-feeding mud star *C. crispatus* comprised a large portion of the abundance.

Biomass in 2012 ranged from 2,801 g wet weight 1000 m^{-2} south of Wrangel Island to 103,876 g wet weight 1000 m^{-2} in the south central Chukchi Sea (Table 1, Figure 2D), with an overall mean of 25,740 ± 25,702 g wet weight 1000 m^{-2}. Overall biomass was dominated by echinoderms with 38% of total

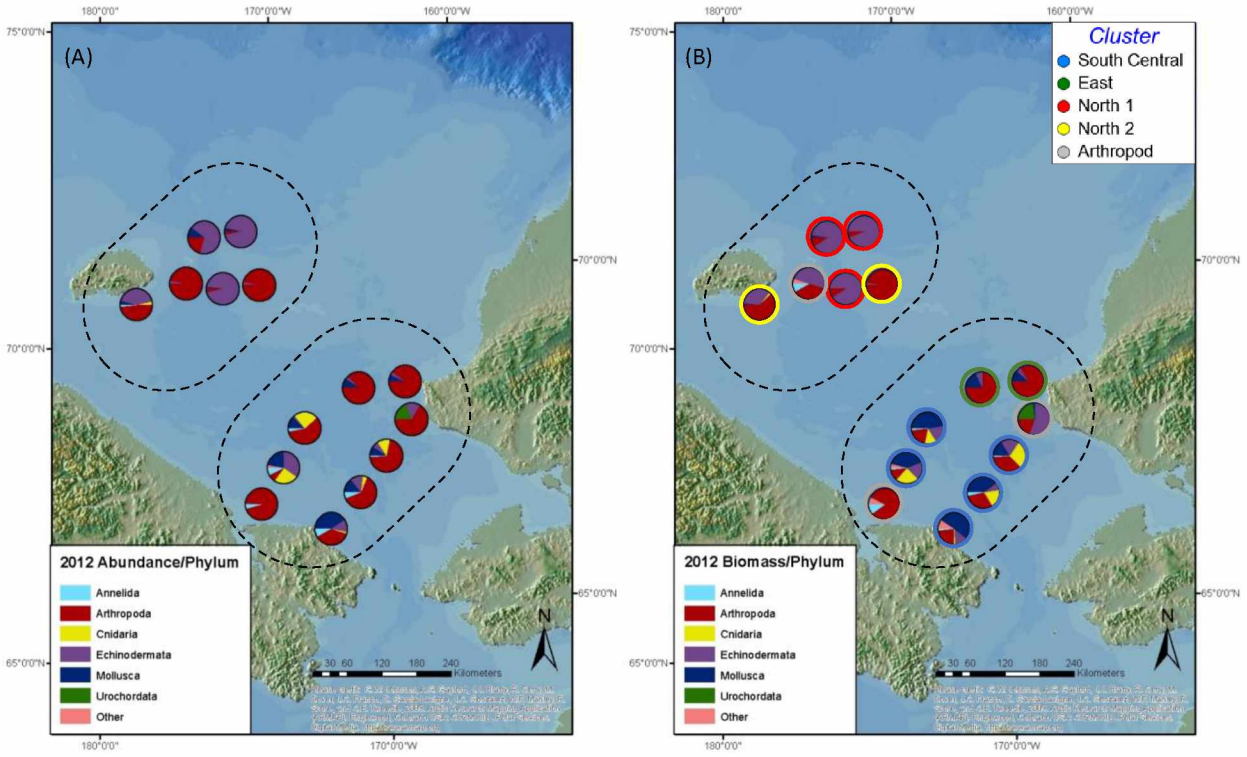

Figure 5. Relative contribution by phylum to epibenthic (A) abundance and (B) biomass per station sampled in 2012. Colored rings around pie charts in Figure 6B denote station clusters identified by hierarchal clustering (group average, 4th-root transformed biomass, Bray-Curtis similarity). Dashed outlines depict northern/southern station groupings.

biomass (mean 9,663 ± 14,056 g wet weight 1000 m^{-2}), followed by arthropods (29%, mean 7,398 ± 8,936 g wet weight 1000 m^{-2}) and mollusks (18%, mean 4,637 ± 6,551 g wet weight 1000 m^{-2}). The mud star *C. crispatus* alone contributed 23% (90,779 g wet weight 1000 m^{-2}) to total biomass even though it only occurred at three stations in the north. The more widely distributed snow crab, *C. opilio,* comprised 14% of total biomass (54,846 g wet weight 1000 m^{-2}). Bulk estimates of biomass did not differ between northern and southern regions (ANOVA p=0.5) although taxa differed in their relative contribution to biomass at each region. At northern stations, echinoderms dominated the overall biomass with 83% (Figure 5B, mean 20,702 ± 20,999 g wet weight 1000 m^{-2}) bolstered by the high biomass of *C. crispatus*. Biomass at southern stations was more evenly distributed among phyla, with arthropods contributing 36%, mollusks 26%, and cnidarians and echinoderms 18% and 16%, respectively (Figure 5B). By functional feeding groups, predators/scavengers made up 48% (185,326 g wet weight 1000 m^{-2}) of the total biomass, while deposit feeders/detritivores contributed 25% (96,525 g wet weight 1000 m^{-2}), but were most common at northern stations.

Five significant station groupings at 30% similarity (SIMPROF, p = 0.05) were identified from the biomass-based community similarity matrix (Figure 6). Stations again grouped in a larger north and south grouping, with reasonably geographically coherent clusters within these two parts. A south central cluster consisted of the majority of southern and central Chukchi stations, an eastern cluster contained two stations off the Alaskan coast of Cape Lisburne. Within two northern clusters, one contained three stations in Herald Canyon (North 1), and another encompassed one southern Herald Canyon station and a station south of Wrangel Island (North 2) (Figure 5B). A fifth group had low similarity (21%) and this group was named "Arthropoda" after the dominant phylum at these stations because stations in this group were geographically disparate (Figure 5B). Because of the low similarity and lack of geographical coherence, this group was excluded from SIMPER analysis (Table 2) and was not considered for further discussion. Average similarity within the other station clusters ranged from 35% to 50% (Table 2). Snow crab, *C. opilio*, was an important contributor to similarity in each of the four geographical station clusters. In addition, the mud star, *C. crispatus*, was responsible for a large portion of the average similarity of the northern Herald Canyon cluster (North 1), while the shrimp *Eualus* sp. and the brittle star *O. sarsii* characterized the cluster North 2. Decapod crustaceans defined the East cluster, with strong contributions from *C. opilio*, the shrimp *Argis* sp., and the hermit crab *Pagurus trigonocheirus* (Table 2). Average dissimilarity among station groupings ranged from 70% to 81%, with *C. crispatus* as the main driver separating the two northern clusters from the rest of the clusters (Table 3).

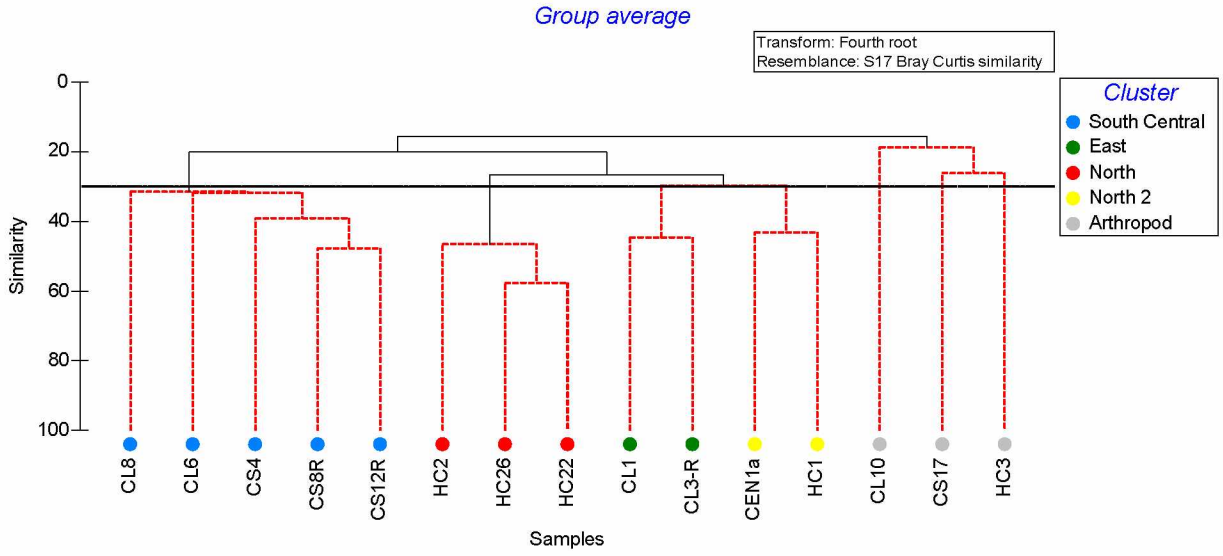

Figure 6. Community similarity identified by hierarchical clustering for stations sampled in 2012. Red dotted lines denote non-significant station groups while black lines indicate significant differences among groups (SIMPROF, p=0.05). Grouping is based on 4th-root transformed biomass resemblance (Bray-Curtis) matrix.

The combination of temperature, latitude, depth, sediment and water column chlorophyll, and percent gravel produced the highest correlation (Spearman rank correlation p=0.524, Table 4) between the fewest environmental variables and the biomass-based community matrix. Percent gravel was the primary environmental driver influencing the epibenthic community structure in the study area, creating nearly as good of a match to community structure as the multivariate combination. However, among bulk biomass measures, only mollusk biomass was significantly (negatively) related to percent gravel. Echinoderm biomass correlated positively to percent mud. Only mollusk biomass was significantly (positive) related to any food supply indicator, namely sediment chlorophyll. No single variable was correlated to both total abundance and biomass, though several variables representing physical hydrographic environmental drivers were correlated to either abundance or biomass (Table 5).

3.1.3. Temporal comparison of community structure over three sampling years

The number of taxa when standardized to the same taxonomic level differed significantly among years (ANOVA, p = 0.01), with 52 taxa in 2004, 49 in 2009, and 72 in 2012. The large increase in 2012 was due to a higher number of suspension feeding taxa. Other functional groups stayed relatively constant across years, with predators/scavengers being the most prominent feeding type in biomass contributions in all years. Average diversity (H') and average evenness (J') did not significantly differ among years (ANOVA, p = 0.42, p = 0.85, respectively).

Total abundance was relatively constant over the three sampling years (Figure 7A). Echinoderms dominated total abundance in 2004 with 64%, mostly with the holothuroid *Myriotrochus rinkii* and the brittle star *O. sarsii*. Echinoderm abundance decreased in 2009 and further in 2012. In contrast, arthropod abundance increased from 2004 to 2012, mostly because of high abundances of the snow crab *C. opilio* in 2009 and increases in *C. opilio*, amphipod and caridean shrimp abundances in 2012. Mollusk abundance peaked in 2009 because of higher numbers of the moon snail *C. affinis* in that year compared with other sampling years.

Total biomass was significantly higher in 2009 than 2012 (ANOVA, p = 0.02) and higher, though not significantly, in 2009 than 2004 (ANOVA, p = 0.06). The low biomass in 2012 was reflected in reduced biomass in all major phyla, except mollusks (Figure 7B). Similar to abundance patterns, echinoderm biomass decreased from 2004 to 2012, mostly due to a decrease in biomass of *O. sarsii* and *M. rinkii*. Arthropod and mollusk biomass both peaked in 2009 due to high biomass of the snow crab *C. opilio* and the moon snail *C. affinis,* respectively. The relationship between abundance and biomass for *C. opilio* in

each sampling year indicates high individual biomass (= large individuals) in 2009 and low individual biomass (= many small individuals) in 2012.

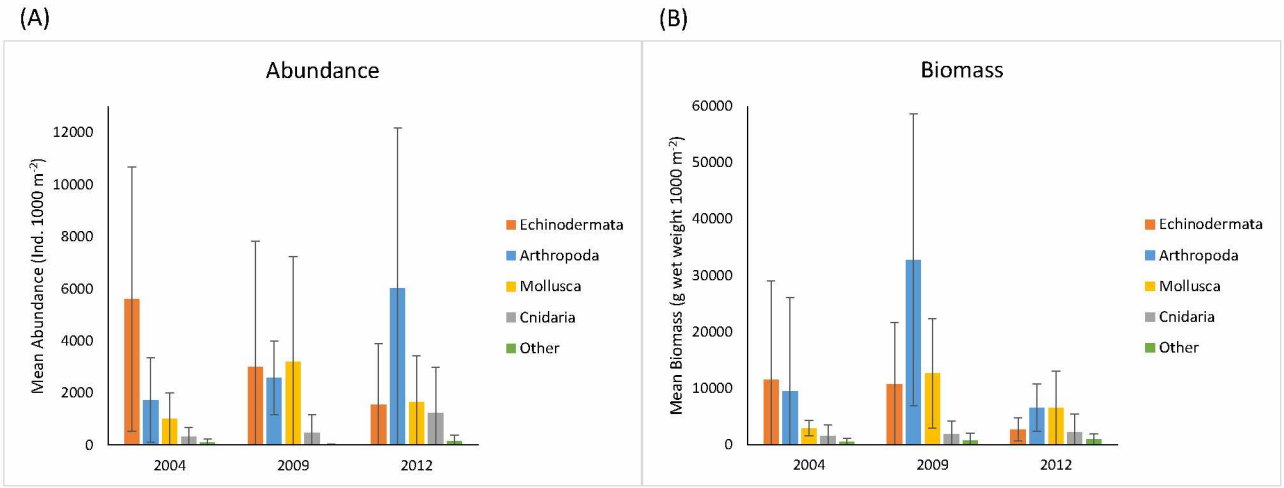

Figure 7. Temporal comparison of mean abundance (A) and biomass (B) per phylum across all stations and water masses in the southern Chukchi Sea.

Stations across years grouped into five distinct epifaunal community clusters at 45% similarity, with stations generally grouping by geographical proximity rather than by sampling year (Figure 8). The clusters observed for repeat stations across all three sampling years were similar to station groupings found during individual sampling years (see sections 3.1 and 3.2). The southwest cluster included all three sampling years of station CS17 on the Alaskan coast, which was also found to be a unique station in the individual sampling years 2009 and 2012. The southeastern Chukchi stations CL1 and CL3 clustered together in both the temporal analysis as well as the individual sampling years. Similarly, the Russian coastal station CL10 grouped together for two of the three sampling years and was also separate from most other south central Chukchi stations in the individual sampling years. The other repeat stations fell into two clusters in the temporal comparison, and most of these stations also clustered together spatially during individual sampling years. ANOSIM results supported distinct groupings when repeat station (high Global R = 0.8, p=0.001) was considered as factor while the factor year (low Global R = 0.1, p= 0.06) showed strong community overlap. This pattern suggests that regions retained relatively consistent epibenthic community composition across the sampling years, despite the at times drastic temporal variability in abundance and biomass.

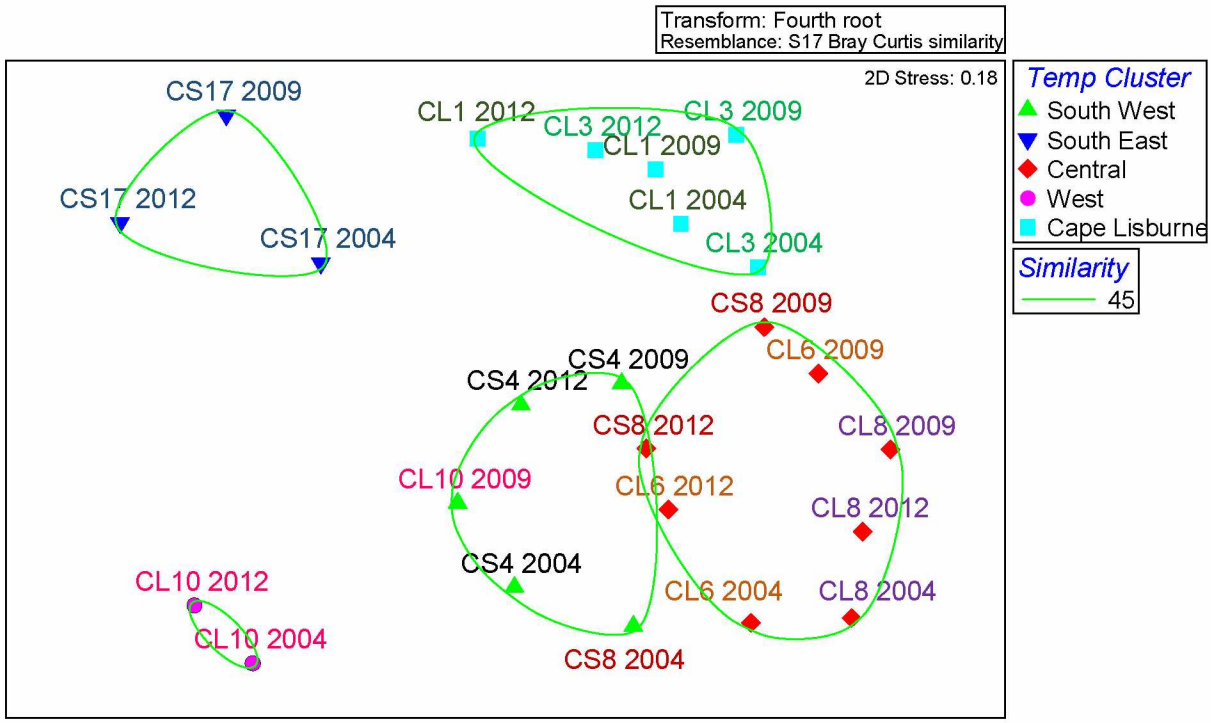

Figure 8. Non-metric multidimensional scaling (nMDS) ordination of repeat (2004, 2009, 2012) stations groups. Groups are outlined at the 45% similarity level as determined by hierarchical clustering. Station names are depicted by colored labels.

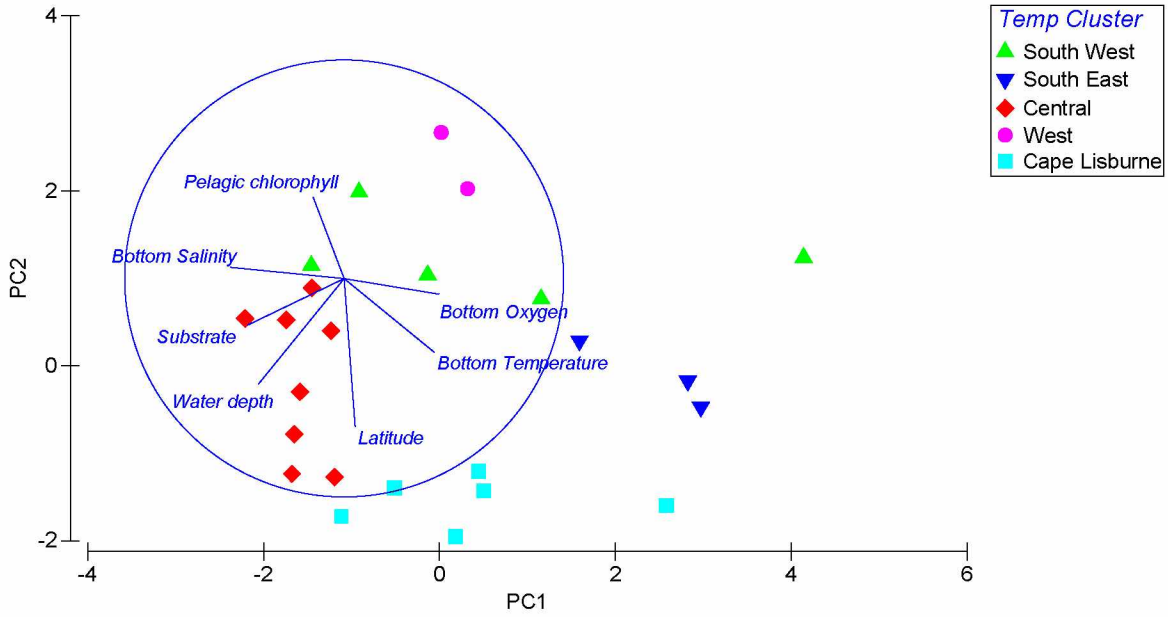

Figure 9. Principal component analysis (PCA) ordination of repeat stations in the southern Chukchi Sea (sampled in 2004, 2009, 2012) based on environmental variables. PC 1 accounts for 44% of the total variance, while PC 2 accounts for 25%. Stations in the PCA were then color coded with group designations from hierarchical cluster analysis of the communities based on a 4th root transformed biomass resemblance matrix (Bray-Curtis).

Across all years, substrate category was the most consistent driver of epibenthic community structure in multivariate analyses (BIO-ENV). Generally, stations ordinated by environmental variables in a principal component analysis (PCA) matched well with biological station clusters (Figure 9), suggesting relatively stable conditions.

3.2. Food web structure

3.2.1 Food web structure in 2009

$\delta^{13}C$ and $\delta^{15}N$ ratios of PPOM were not significantly different (ANOVA, $p \geq 0.05$) among the three water masses in 2009. Insufficient sediment samples were available to be analyzed statistically for differences in isotope values among water masses, although SPOM $\delta^{13}C$ and $\delta^{15}N$ values were higher in BSAW than other water masses (Figure 10A and B).

Total food web length varied among water masses with longer food webs in ACW than in either RC or BSAW. When all sampled organisms were considered, those in BSAW and at the RC station each covered a total $\delta^{13}C$ range of 7‰ while those in the ACW spread over a range of 12‰. Taxa from BSAW were significantly enriched in ^{13}C when compared with the same taxa at RC (ANOVA, $p = 0.037$), while differences for the same taxa between BSAW and ACW were marginally not statistically significant ($p = 0.051$, Figure 10A), although those differences might still be biologically relevant. The overall $\delta^{15}N$ range of ACW organisms (9‰) was also higher than that of either BSAW or RC organisms (7‰ and 5‰, respectively). There were no significant differences in nitrogen isotope signatures of organisms among water masses (ANOVA, $p > 0.05$, Figure 10B).

The community in ACW had five trophic levels compared with four trophic levels in either RC or BSAW (Figure 10C). Most taxa in ACW were at trophic levels 4 and 5, while less than 20% of all taxa contributed to taxon numbers at trophic levels 2 and 3. In contrast, taxa in both BSAW and RC were 90% and 70% at trophic levels 1 and 2, respectively, with the remaining taxa at trophic level 4 in both water masses (Figure 10C). In terms of biomass, taxa in trophic levels 4 and 5 contributed the majority of epibenthic biomass in ACW (~75%, Figure 10D), while the lower trophic level (2 and 3) taxa were not represented by epibenthic biomass, i.e., they were infaunal and pelagic taxa. About 25% of the epibenthic biomass in ACW was not allocated to a specific trophic level because no isotope data were measured for those taxa. In contrast, nearly 88% of the total epibenthic biomass in BSAW was comprised of organisms occupying trophic level 3, represented mostly by the snow crab *C. opilio*. In contrast to trophic level 3 in BSAW, this species fed at trophic level 4 in ACW and at the RC station. In RC, the majority of the epibenthic biomass

was represented in trophic level 4, particularly driven by the large biomass of the crabs *C. opilio* and *Hyas coarctatus.*

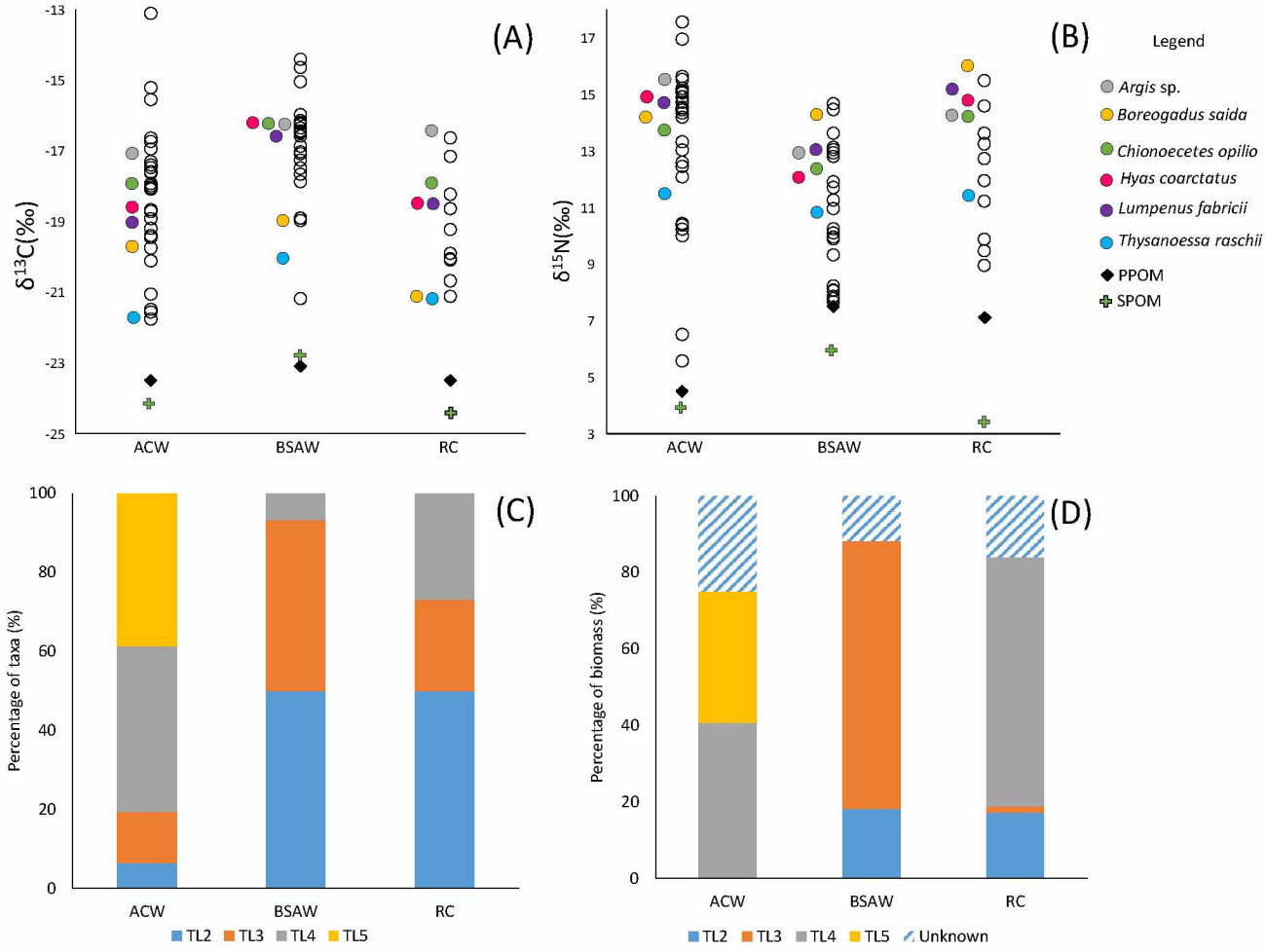

Figure 10. Stable isotope values and food web structure of PPOM, SPOM, pelagic and benthic invertebrates, and demersal fishes sampled in 2009. (A) $\delta^{13}C$ values of organisms and POM, (B) $\delta^{15}N$ values of organisms and POM; colored circles denote common taxa among all three water masses, open circles represent the remaining taxa in each water mass. (C) Proportional contribution of number of taxa to trophic levels and (D) proportional contribution of biomass to trophic levels. Taxa for which no stable isotope data were available were classified as unknown. PPOM was used as the baseline for trophic level calculations (see text for details). (ACW) Alaskan Coastal Water, (BSAW) Bering Shelf-Anadyr Water, (RC) Russian Coast. TL= Trophic Level.

3.2.2. Food web structure in 2012

$\delta^{13}C$ and $\delta^{15}N$ values of PPOM did not differ among the three water masses in 2012 (ANOVA, $p > 0.05$), with either isotope ratio differing no more than 1.5‰ among water masses. In all water masses, SPOM was either similar (RC) or slightly enriched in ^{13}C and in ^{15}N compared with PPOM, but insufficient replicate sediment samples did not allow confirming the statistical significance of these patterns.

Organisms in BSAW had significantly higher $\delta^{13}C$ (ANOVA, $p = 0.037$) and lower $\delta^{15}N$ (ANOVA, $p = 0.048$) values when compared with their ACW conspecifics (Figure 11A and B, respectively). Organisms in RC were not significantly different in either nitrogen or carbon stable isotope values when compared with BSAW or ACW (ANOVA, $p > 0.05$ for both comparisons).

In contrast to 2009, total food-web length was similar across water masses, with food webs comprising five trophic levels in each water mass (Figure 11C). The majority of taxa sampled were within trophic level 4 in all water masses, while trophic level 2 taxa only occurred in RC and BSAW. In ACW and BSAW, organisms occupying trophic levels 3 and 4 were ≈20 - 50% of the epibenthic biomass, with a much smaller contribution to trophic level 5 when compared with RC. In RC, the majority of the epibenthic biomass was concentrated in trophic levels 4 and 5, mostly because of high biomass of the shrimp *Eualus* sp. (TL 4) in that water mass. Stable isotope, and thus trophic level information, was not available for a large number of taxa in ACW, resulting in a large portion of the biomass classified as "unknown" trophic level. In all water masses, trophic level 2 was not well represented in the epibenthic biomass in this year, despite accounting for a large portion of the taxa sampled for stable isotopes, particularly in BSAW and RC, because trophic level 2 biomass was comprised of infaunal and pelagic taxa.

3.2.3 Temporal comparison of food web structure over three sampling years

Neither stable carbon nor nitrogen isotope ratios of PPOM or SPOM significantly differed among years within any of the three water masses due to high variability within each year. Differences in carbon isotope ratios between SPOM and PPOM did not follow any distinct pattern; however, PPOM was always enriched in ^{15}N when compared with SPOM in 2004 and 2009, but depleted compared with SPOM in 2012 (Figure 12). In all years in ACW, there was a noticeable gap in $\delta^{15}N$ values between PPOM and epibenthic consumers (Figure 12F) that was occupied by very few taxa (e.g., ascidians, pelagic cnidarians). This gap indicates that the majority of consumers in ACW did not consume the PPOM food

source directly and suggests consistently missing trophic links not represented in the benthos. This gap was not present in the BSAW communities and not as pronounced at the RC station.

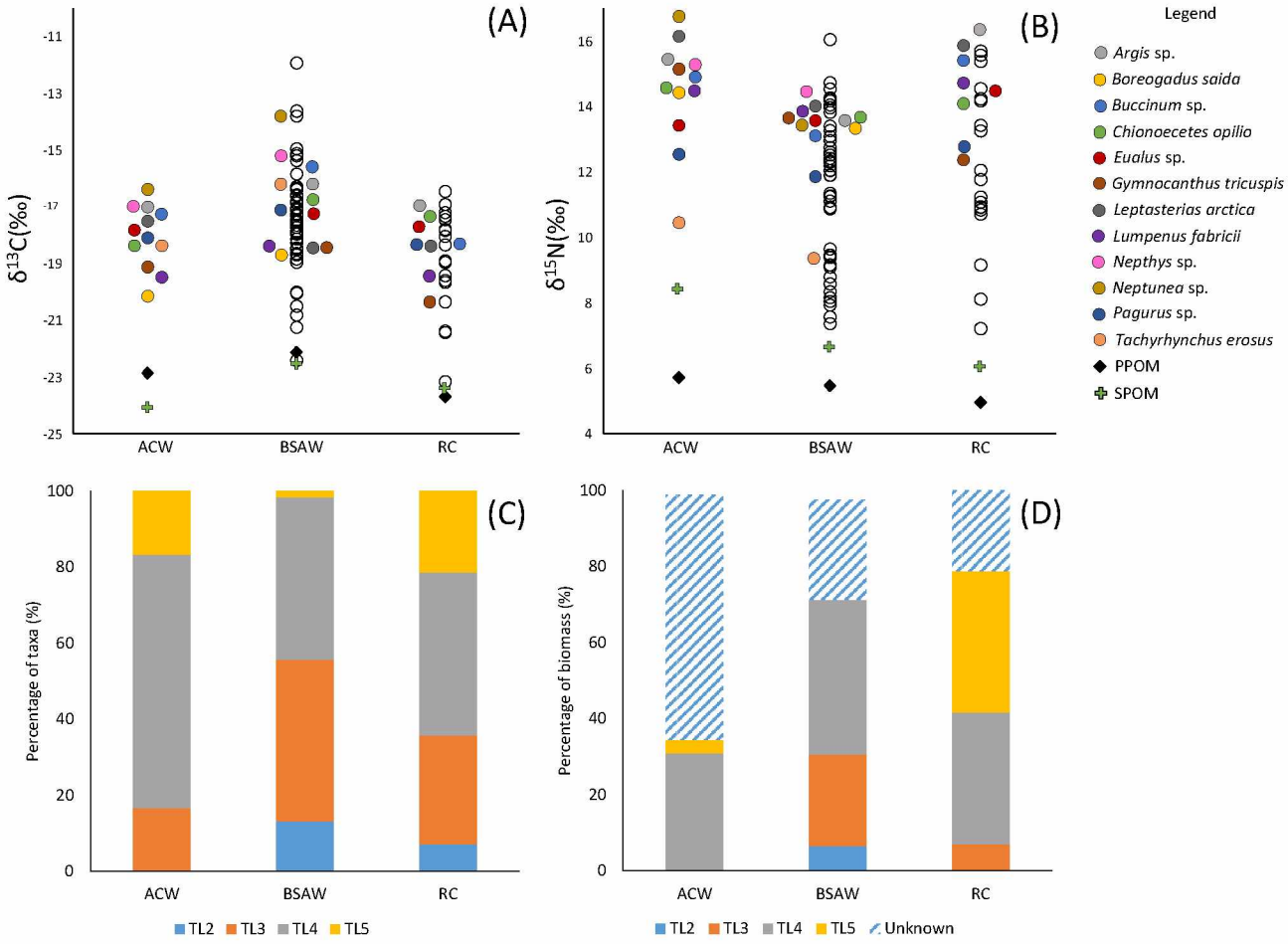

Figure 11. Stable isotope values and food web structure of PPOM, SPOM, pelagic and benthic invertebrates, and demersal fishes sampled in 2012. (A) $\delta^{13}C$ values of organisms and POM, (B) $\delta^{15}N$ values of organisms and POM, colored circles denote common taxa among all three water masses, open circles represent the remaining taxa. (C) Proportional contributions of number of taxa to trophic levels and (D) proportional contribution of biomass to trophic levels. Taxa for which no stable isotope data were available were classified as unknown. PPOM was used as the baseline for trophic level calculations. (ACW) Alaskan Coastal Water, (BSAW) Bering Shelf-Anadyr Water, (RC) Russian Coast. TL= Trophic Level.

Carbon isotope values of the same taxa differed significantly among years within RC (ANOVA, $p = 0.028$), with significantly higher values in 2004 than 2009 ($p = 0.015$) and 2012 ($p = 0.025$) (Figure 12A). Nitrogen isotope values in RC, however, did not differ among years (ANOVA, $p = 0.18$) (Figure 12B). In ACW and BSAW, neither carbon nor nitrogen isotope values of the same organisms differed significantly among years (ANOVA, $p > 0.05$ for all comparisons) (Figure 12C-F).

Taking all sampled taxa into account, the food web in ACW was longest with six trophic levels (although only one taxon, an anemone, was in trophic level 6) in 2004 and five trophic levels in 2009 and 2012 (Figure 13A). In BSAW, the food web was the shortest in 2009 (four trophic levels), while food web lengths were similar in 2004 and 2012 with five trophic levels (Figure 13B). In RC, the food web was longer in 2012 (five trophic levels) than in previous sample years (four trophic levels). Most (>80%) taxa analyzed for food web structure in ACW were in trophic levels 4 and 5 in all years, with the remaining taxa mostly within trophic levels 3 and very few in trophic level 2 (Figure 13A). In contrast, the majority of the taxa in BSAW were in trophic levels 2-4 in all years; however, proportionally much fewer taxa were at trophic level 4 in 2009 than the other two sampling years, especially in 2012 (Figure 13B). Similar to BSAW, most taxa in RC were within trophic levels 2-4, and only in 2012 about 20% of the taxa were at trophic level 5 (Figure 13C).

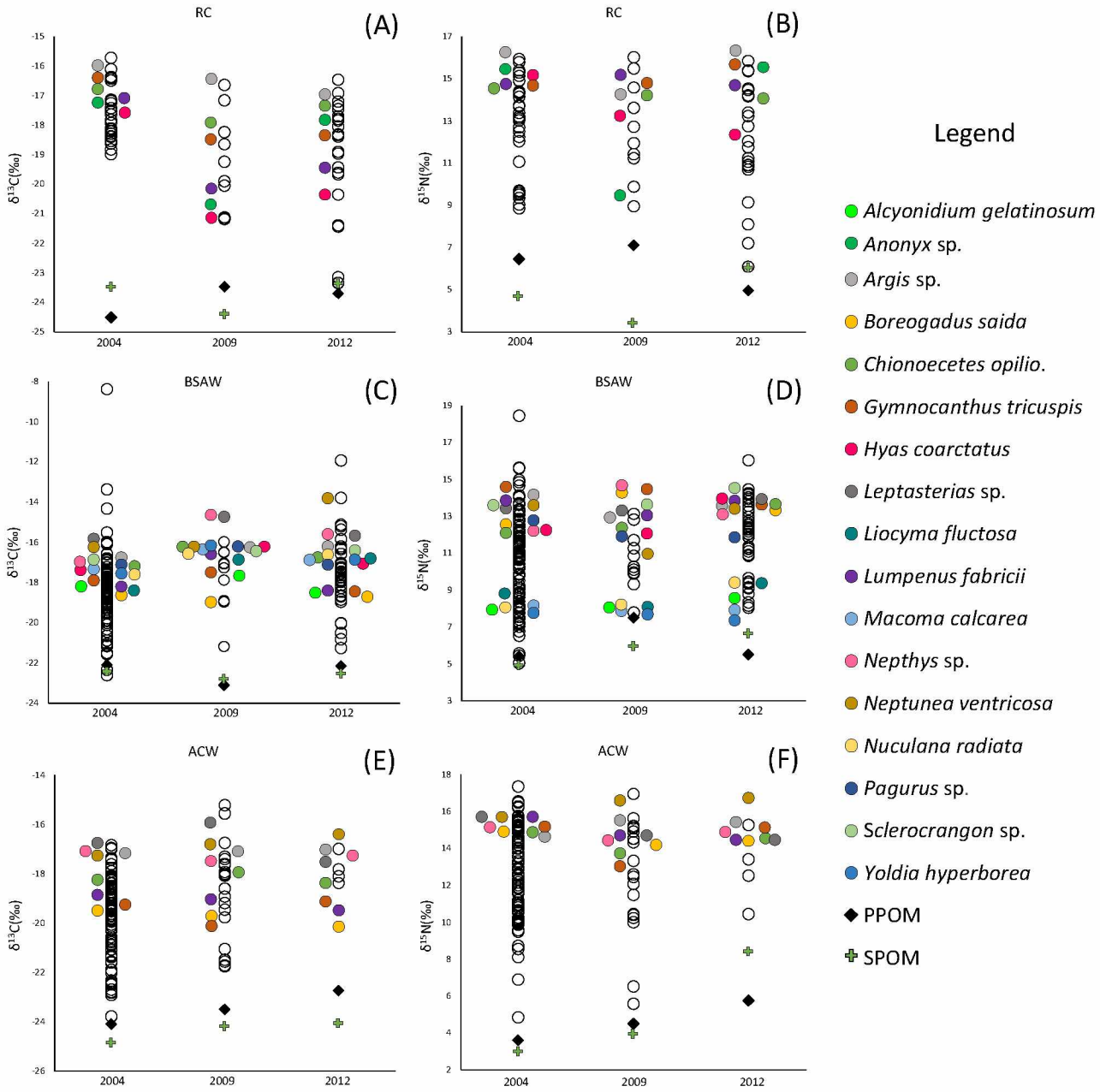

Figure 12. Temporal comparison of $\delta^{13}C$ and $\delta^{15}N$ values of organisms and particulate organic matter (POM) sampled repeatedly in 2004, 2009 and 2012 within water masses in the southern Chukchi Sea. Colored circles represent common taxa, open circles represent the remaining taxa in each water mass.

4. Discussion

Consistent spatial patterns in epibenthic community structure were observed in 2009 and 2012, reflecting biogeography and the influence of environmental forcing, despite some differences in station coverage (Section 4.1). While some of these overall community composition patterns persisted over all sampling years where identical stations were sampled repeatedly, temporal variation in the quantitative contribution of some taxa to community structure and in total abundance and biomass were found (Section 4.2). Spatial patterns in benthic food web structure in the southern Chukchi Sea differed among water masses (Section 4.3), and these differences were relatively consistent between 2004, 2009 and 2012 (Section 4.4).

4.1. Spatial patterns in epibenthic community structure

Community distribution patterns reflect a combination of environmental conditions, biological interactions, and biogeography. Epibenthic communities clustered into regionally distinct spatial groups, and while specific clusters between the study years 2009 and 2012 cannot be directly compared, the general distribution of community clusters across the Chukchi shelf in both years offers insight into spatial community patterns and their potential drivers. Consistently within the 2009 and 2012 study years, epibenthic communities differed in total abundance and biomass and in structure between the northern and the southern study regions, with somewhat variable subgroupings within each of those larger regions. These north and south groupings reflect known biogeographical regions reasonably well. Epibenthic communities in the Chukchi Sea represent a transition zone between the Arctic and North Pacific oceans, with the southern Chukchi Sea characterized by boreal and boreal-subtropical communities and a gradual poleward increase in the occurrence of Arctic and boreal-Arctic fauna (Petryashov et al. 2013). In addition to historical biogeography, the distinction between northern and southern shelf communities likely reflects a response to latitudinal patterns in environmental conditions. While latitude is not a forcing mechanism in itself, it is representative of the environmental variables with which latitude may co-vary (i.e., depth, seasonally changing solar radiation, water mass characteristics, and ice cover) (Hawkins & Felizola Diniz-Filho 2004).

Within the northern shelf region, epibenthic communities differed between those around Wrangel Island (the Northwest cluster in 2009, Figure 3B) and those associated with Herald Canyon (clusters North 1 and North 2 in 2012, Figure 5B). Communities around Wrangel Island included stations on the East Siberian shelf (sampled in 2009) where Pacific-derived waters meet with local, cold shelf water

from the East Siberian Sea (Semiletov et al. 2005). The influence of this cold water mass likely contributed to the distinction of the epibenthic community in this region, which differed from all other study regions by large numbers of boreal-Arctic species such as the brittle star *Ophiocten sericeum* and the arctic isopod *Saduria* sp., the latter of which is common in the East Siberian Sea (Petryashev 2002, Grebmeier et al. 2006, Petryashov et al. 2013). Together with the northern Chukchi shelf, the East Siberian shelf is generally considered to be a different biogeographical province than the southern and central Chukchi shelf (Mironov 2013). The East Siberian shelf is a shallow shelf that receives runoff from numerous rivers, including the Kolyma River, the fifth largest river draining into the Arctic Ocean (Holmes et al. 2012). Benthic communities near major river drainages are heavily influenced by freshwater and the input of terrestrial material, factors that favor species tolerant to those conditions (Schmid et al. 2006, Semprucci et al. 2010). Although the communities around Wrangel Island were not directly adjacent to the Kolyma River delta, the dominant epibenthic taxa found in this study were more similar to those found on river-influenced shelves in the Laptev (Piepenburg & Schmid 1997) and Beaufort seas (Roy et al. 2014) than to those in the northern and central Chukchi Sea (Feder et al. 2005, Ravelo et al. 2014, present study). Hydrographic data collected concurrently with trawl surveys in the present study showed a distinct freshwater signal overlying the East Siberian and northwestern Chukchi shelf (data available at http://www.whoi.edu/science/po/pickart/newFieldPrograms.htm). This suggests that the epibenthic communities around Wrangel Island, especially those on the eastern East Siberian shelf, may be affected by river run-off similar to those found on other river-influenced shelves.

Communities associated with Herald Canyon in the northwestern Chukchi Sea differed in both years from communities found around Wrangel Island, with a larger portion of species of Pacific origin in the Herald Canyon area, although still more arctic in character than those in the southern Chukchi Sea (Krylova et al. 2013, Petryashov et al. 2013). Communities around Herald Canyon were characterized by high densities of either suspension or deposit feeders, depending on location. Particularly, the deposit-feeding mud star *Ctenodiscus crispatus* occurred at high biomass near the Chukchi shelf break, which was also reported for the epibenthic community in this region in 2004 (Bluhm et al. 2009). The assemblages in Herald Canyon may be taking advantage of the food supply associated with the water flow moving through the canyon (Pickart et al. 2010). Nutrient-rich BSAW advected through Bering Strait moves northwards across the Chukchi Sea and in part flows out through Herald Canyon (Coachman et al. 1975, Walsh et al. 1989). On the eastern flank of Herald Canyon, the flow is consistently poleward and swift, whereas on the western side, the flow is decidedly weaker and more variable (Woodgate et al. 2005, Pickart et al. 2010). Some of the advected organic material originating from phytoplankton and ice

algal blooms upstream may settle to the benthos in the weaker flow regions of western Herald Canyon, providing a food source for deposit feeding epifauna. In contrast, suspended particles advected through the high-flow, dynamic areas and re-suspended particles can provide a food source for suspension feeding organisms, such as ascidians, bryozoans and sponges (Bluhm et al. 2009, present study). Soft-bottom communities are typically dominated by deposit feeding or burrowing organisms from various taxa (Lanihan & Micheli 2001, Byers & Grabowski 2013). Interestingly, however, suspension-feeding ascidians made up a large portion of the biomass at one northern Herald Canyon station where soft sediments were prevalent, likely due to a slowing of current speed near western flank of the canyon (Pickart et al. 2010). Large assemblages of sessile suspension feeders on soft sediments such as in Herald Canyon are also known to occur on soft sediment in temperate and other polar seas (McKinney 2003, Gili et al. 2006), where dense populations may facilitate larval recruitment by acting as "ecosystem engineers" (Jones et al. 1996) that stabilize the soft substrate (Gili et al. 2006), or themselves provide patches of hard surfaces on soft sediment (Yakovis et al. 2005).

Two stations flanking the region immediately south of Herald Canyon (North 2, Figure 5) were distinguished from other northern stations by large biomass contributions by crustaceans, especially the snow crab, *Chionoecetes opilio*. This large snow crab biomass may represent the northern extent of a region in the north-central Chukchi Sea that is dominated mostly by arthropods, particularly snow crabs (Ravelo et al. 2014). The distribution of these crabs may be related to rich food supply associated with transport along the Chukchi Sea Central Channel (Hardy et al. 2011, Ravelo et al. 2014) and may be limited in its northern extent by bottom water temperature (Bluhm et al. 2009). Snow crab are commonly found at temperatures ranging between 0 and 1°C and are physiologically restricted to waters colder than 5°C, but energetically "break even" in waters around 1°C and experience slight negative growth at colder temperatures (Foyle et al. 1989). Temperature conditions affect reproduction, recruitment and distribution of the species (Taylor & O'Keefe 1986, Foyle et al. 1989). This is consistent with the distribution of snow crab in the present study, where fewer snow crab occurred at northern stations in the Herald Canyon area where temperatures at stations averaged -0.3 and -0.8°C during sampling, and snow crab were more abundant at stations in the south central Chukchi Sea region where average temperatures were 1.4 and 2.6 °C (2009 and 2012, respectively).

The southern Chukchi Sea region differed from the northern region by a larger portion of Pacific-boreal species (e.g., Golikov 1989). The central Chukchi epibenthic community (stations CL3, CL6, CL8, CS12, CS8) differed in both study years from communities along the Alaskan (CL1, CS17) and the Russian (CL10,

CS4) coasts and was characterized by a large biomass of predators-scavengers, especially the snow crab *C. opilio* and the predatory gastropod *Cryptonatica affinis.* The panmictic population (Albrecht et al. 2014) of *C. opilio* in general is a major contributor to epibenthic biomass in the northern Bering and southern Chukchi seas (Grebmeier et al. 2006, Bluhm et al. 2009, present study), the central to northeastern Chukchi shelf (Bluhm et al. 2009, Blanchard et al. 2013, Ravelo et al. 2014), and into the western Beaufort Sea (Rand & Logerwell 2011, Ravelo et al. 2015). Although the National Marine Fisheries Service (NMFS) Arctic Fisheries Management Plan does not currently deem a sustainable commercial snow crab fishery in the Alaskan Arctic feasible (NPFMC 2009), this population may support future commercial interests. High prey densities are needed to support high densities of predatory snow crab (Kolts et al. 2013), and the strong aggregation of snow crab in the southern Chukchi Sea may thus be related to a macrobenthic "hotspot" (*sensu* Grebmeier et al. 2015) of infaunal prey on the central shelf. Infaunal bivalves common at the "hotspot" location also are one of the dominant prey items for snow crab (Kolts et al. 2013, Divine et al. in review). This matches the results of the present study where some measures of food availability (i.e., infaunal biomass, sediment and water column chlorophyll) were found to be important drivers of epibenthic community composition in 2009 and/or 2012. Several other crab species, such as the lyre crab *Hyas coarctatus*, were also present at a majority of central and coastal stations in the southern study region, but were not dominant in any of these sub-regions. Where *C. opilio* and *H. coarctatus* co-occurred, one species was always dominant over the other, typically exceeding the abundance and biomass of the subordinate taxon by at least one order of magnitude. This inverse relationship was more common in coastal regions, where the large density of crabs may create stronger competition for food because the two taxa have similar feeding habits (Wieczorek & Hooper 1995).

Benthic communities in the south central Chukchi Sea in this study also had high biomass of mollusks as found earlier for the same study region (Bluhm et al. 2009). Particularly the predatory moon snail *Cryptonatica affinis* was at times dominant in the south central study region, which again appears to overlap with the macrobenthic "hotspot" region (Grebmeier et al. 2006). The macrobenthos community there harbors dense populations of infaunal bivalves, dominated by *Macoma calcerea* (Sirenko & Gagaev 2007), which is an important food source for *C. affinis* (Feder et al. 1994). This "hotspot" region of high infaunal biomass suggests temporally consistent organic carbon deposition, and reflects the high primary production in the southern Chukchi Sea (Grebmeier et al. 1988) that escapes zooplankton grazing and supports benthic production (Grebmeier & Barry 1991, Grebmeier et al. 2006). While I did not find a significant relationship between overall mollusk biomass and infaunal biomass in the 2009

analysis, individual taxa such as moon snails may still respond to this abundant prey supply in a particular region.

Inshore epibenthic communities along both eastern and western margins of the southern Chukchi Sea are influenced by river run-off and coastal currents shaping the Alaskan and Russian coastal domains, (Carmack et al. In press). Communities along these coasts with comparable substrate type are functionally similar, e.g., dominated by suspension feeders where hard substrate is available (Feder et al. 2005), but are taxonomically distinct. Communities in the southeastern region along the Alaska coast are subject to the variable influx of freshwater and terrestrial matter transported in the ACW, derived mostly from Yukon River discharge in the Bering Sea (Coachman et al. 1975, Striegl et al. 2007). Mixed into this, phytoplankton and marine organic carbon may be laterally advected from the more productive south central Chukchi Sea (BSAW) into the inshore regions and under the ACW (Feder 1990, Hunt & Harrison 1990, Feder et al. 2005, Grebmeier et al. 2006). Earlier studies argued such processes would provide a plentiful food source for the coastal benthos and maintain benthic populations much larger than would be expected under the typically nutrient poor conditions of the ACW (Feder et al. 2005, 2007, 2011). In the present study, those Alaska coastal communities were characterized by the basket star *Gorgonocephalus* sp., a euryhaline suspension feeder (Emson et al. 1991) that can tolerate the variable environment created by the seasonal freshwater input from coastal sources and the physically dynamic substrate structure influenced by wave action and ice scouring (Woodgate & Aagaard 2005). Stations on the Russian coast of the Chukchi Sea where hard substrate was prevalent were also colonized by sessile suspension feeders, but were characterized by colonial forms such as sponges, ascidians and bryozoans rather than the large-bodied organisms which were common on the Alaskan Coast. However, these suspension feeders were not biomass-rich enough to be indicator taxa for the community, and hard substrate was not representative of the entire western region. Instead, the deposit-feeding holothurian *Myriotrochus rinkii* represented a large portion of the biomass at the western coastal community group. The *Myriotrochus* community was common in the western coastal areas where small grain size dominated and organic carbon content is known to be high (Grebmeier et al. 2006) and where indicators of food availability and sediment characteristics correlated well with community composition. The abundance of deposit-feeding holothurians is influenced by food availability, specifically the quality of food (Wigham et al. 2003). For example, deep-sea holothurians can selectively exploit pulses of "fresh" phytodetritus (Wigham et al. 2003, Billett et al. 2010). Juvenile holothurians in particular may be selective towards habitats with substrates of smaller grain size and high organic matter content, as observed in nearshore environments (Mercier et al. 2000).

4.2. Temporal patterns in community structure and environmental drivers

Overall epibenthic community composition in the southern Chukchi Sea stayed relatively consistent over the time period considered in this study while estimates of abundance and biomass were at times highly variable. The relative temporal stability in overall epibenthic community structure in the face of environmental variability either reflects that indeed no detectable, substantial change of the community occurred, or that change occurred but the patterns were not detected in this study. Variability in epibenthic community structure can manifest at various temporal and spatial scales. The detectability and interpretation of community patterns is in part dependent on the frequency and spatial extent of sampling. For example, a shift in epibenthic community composition related to changes in oceanographic conditions was detected after only ten days (from shrimp to gastropods) during high-frequency sampling off of the coast of Vancouver Island, Canada (Matabos et al. 2014). Conversely, a 24-year study of benthic community structure in the Northeast Pacific revealed a decadal-scale cycle in the composition of benthic fauna that was only detectable with long-term observation (Kuhnz et al. 2014). It is possible that the present study failed to detect shifts in community structure that may have occurred at scales not captured by the design of this study (e.g., at shorter or longer time periods, at smaller or larger spatial coverage). Evidence for this may be found in the fact that abundance of some taxa changed quite drastically among sampling events, and it is possible that with higher sampling frequency or more intense spatial coverage per water mass, temporal patterns in overall community structure may have been revealed.

4.2.1 Stability of epibenthic community structure

The finding of relatively stable epibenthic community structure between 2004 and 2012 agrees with earlier studies that reported on the temporal persistence of epibenthic community structure on the Chukchi Sea shelf over decadal time scales despite abundance and biomass increases for several dominant taxa, at least since the late 1970s (Feder et al. 2005, Bluhm et al. 2009, Powell 2015). This seems to indicate that the spatial distribution of community composition is mostly driven by relatively persistent environmental conditions on decadal scales despite the typically strong seasonal variability in the Arctic environment. In the present study, most dynamic environmental variables that fluctuate on multiple time scales from days to seasons to years (e.g., salinity, oxygen, temperature, etc.) were not regularly correlated to the epifaunal matrix over sampling years. The point sampling of these metrics in

this study certainly did not capture their value range significantly (see for example temperature ranges in Grebmeier et al. 2015). In contrast, the more temporally stable measures of substrate type were most consistently identified as drivers of epibenthic community structure across all three sampling years, while depth and latitude were influential when each sampling year was analyzed separately. Together, these latter factors represent a suite of comparatively stable environmental drivers although sediment grain size can change in response to hydrographic conditions with possible effects on the benthic community (Moore et al. 2003).

Sediment grain size has long been known to structure benthic communities, particularly infaunal communities, both through its links to organic carbon content (i.e., food supply) and to habitat structure (Grebmeier et al. 1989, Gray 2002). Similarly, substrate type is an important factor governing the composition of epibenthic assemblages in the Chukchi and Beaufort seas (e.g., Bluhm et al. 2009, Ravelo et al. 2014, Roy et al. 2014). In the present study, bulk estimates of abundance and biomass were mostly positively correlated with the presence of fine sediment, although not all of these correlations were statistically significant. In contrast, coarser substrates were negatively correlated to those same metrics (Table 5). The mechanisms governing the relationship between epibenthic communities and substrate type may vary by taxa and functional groups (Bluhm et al. 2009). The majority of taxa sampled in the present study were mobile predators/scavengers whose life history strategy may not be strongly associated with a particular substrate type (Bluhm et al. 2009) In comparison, sessile organisms that rely on hard substrate for attachment (e.g., bryozoans, hydrozoans) or grazing (e.g., sea urchins) were not well represented in the biomass, due to the prevalence of soft substrate in the study region. Sediment grain size distribution generally reflects hydrographic conditions and as such often co-varies with other environment factors. For example, suspension feeding organisms, like the basket star *Gorgonocephalus* sp., represented a large portion of the biomass at stations with coarse substrate, such as those on the Alaskan coast where swift currents can be present (Overland & Roach 1987) and suspended particles may provide a rich food source. The slowing currents in the central Chukchi Sea after exiting Bering Strait coincide with the presence of soft substrate, which was positively correlated with organic carbon content in 2009 (data not shown). These conditions favor an area of persistent carbon deposition, creating the abovementioned "hotspot" of infaunal biomass (Grebmeier et al. 2006) that can support a high biomass of mobile predators. Thus, while substrate categories were a prominent and consistent predictor of epibenthic community composition, the relationship is likely to represent a host of biotic and abiotic interactions rather than sediment grain size alone.

Similar to grain size, latitude represents a host of environmental conditions acting in concert to shape epibenthic community composition rather than acting as a driving mechanism in itself (Hawkins & Felizola Diniz-Filho 2004). The observed poleward shift in biomass dominance from arthropods to echinoderms likely reflects a combination of biological interactions and environmental forcing. Ophiuroids, the dominant echinoderm group in the present study, form dense aggregates in areas where there is low predation pressure (Fujita & Ohta 1989, 1990). The large biomass of ophiuroids in the northern stations may be relieved from predation pressure in the absence of large populations of snow crab (present study) and demersal fish (Barber et al. 1997), both predators of ophiuroids (Packer et al. 1994, Wieczorek & Hooper 1995, Divine et al. in review).

Depth also is a static environmental variable that can affect epibenthic community structure, mostly indirectly. While patterns of depth zonation are particularly important in deep-sea and continental slope communities (Levin et al. 2001, Howell et al. 2002), depth-driven zonation is also apparent in Arctic shelf communities (Piepenburg & Schmid 1996), and on small scales in the Chukchi Sea (Blanchard et al. 2013). Physiological factors are unlikely to impose depth range limits on the shallow shelf of the Chukchi Sea, where overall sampling depth range was just from 33-74 m, excluding two deeper stations in Herald Canyon that were as deep as 152 m. The indicator taxa of the two main north/south groupings, *O. sarsii* and *C. opilio* respectively, are likely not limited in their distribution by depth in the study region. Snow crab are commonly found from 20 to 500 m deep in the Chukchi and adjacent Beaufort Sea (Logerwell et al. 2011) and 100 to 200 m in the Bering Sea (Zheng & Kruse 2006) and *O. sarsii* occur in large numbers at depths ranging from around 30 to 210 m (Ambrose et al. 2001, Bluhm et al. 2009). Instead, correlations between epibenthic community structure and depth may represent environmental variables that co-vary with depth in the Chukchi Sea, such as temperature (previously discussed), increased food deposition in slightly deeper regions (Blanchard et al. 2013) as well as differences in hydrography with depth (e.g., Kostylev et al. 2001). Depth was also positively correlated with sediment organic carbon content, and the geographic location of the deeper stations (i.e., Herald Canyon) may indicate that epibenthic communities were influenced by other variables associated with Herald Canyon, such as biogeography and environmental factors related with its northern latitude or physical characteristics.

It is curious that hydrographic variables (e.g., temperature, salinity) *per se* did not seem to have a strong influence on the overall community structure in the southern Chukchi Sea during the study years, although these environmental drivers can vary over annual to decadal time spans as were considered in

this study. The Chukchi Sea receives significant freshwater and heat input from the Bering Sea and North Pacific (e.g., >1/3 of total freshwater input into the Arctic) (Woodgate & Aagaard 2005) and this heat flux through Bering Strait doubled between 2001 and 2007 (Woodgate et al. 2010), coinciding with much of the time period of this study. Marginal seas have experienced the greatest reduction in sea ice cover among Arctic seas (Frey et al. 2014). In the Chukchi Sea, changes in the sea ice regime and warming waters are reflected in altered patterns of primary production (Arrigo et al. 2008, Grebmeier 2012), and changes in phytoplankton community size structure were found in the Canada Basin and North Atlantic (Li et al. 2009, Morán et al. 2010). Such changes in the size structure of primary producers may have consequences for size-selective pelagic grazers, whose community composition and trophic dynamics are sensitive to particle size and food availability (e.g., Fuchs & Franks 2010). Increased sea surface temperatures may also impact zooplankton communities by altering temperature-mediated distribution of some taxa (Beaugrand et al. 2002) or by affecting the phenology of zooplankton production, which may be sensitive to warming (Richardson 2008). Modifications in the zooplankton community composition or biomass could alter the amount of food exported to the benthos, either by increased grazing on phytoplankton producers, or by a reduced export of fecal pellets and zooplankton carcasses. Epibenthic community composition could then be affected through altered energy pathways in abundance, biomass, or distribution and composition of taxa. It could be assumed that hydrographic variations also affect local epibenthic communities through new immigrants from the North Pacific (e.g., Węsławski et al. 2011, Nelson et al. 2014). Indeed, new crustacean and bivalve epibenthic immigrants from the North Pacific have been recorded in the southern Chukchi Sea in low numbers during the study period (Sirenko & Gagaev 2007) and various fish and invertebrates in the Bering Sea have extended their centers of distribution northward (Mueter and Litzow 2008). It may be that these new arrivals have not yet altered the existing community composition because they expand their range at low rates early in their dispersal, and increase the rate of invasion as time passes (Ruiz et al. 2000). Also, depending on the competitive ability of new immigrants, they may or may not be able to outcompete existing species and thereby cause a community change.

It is possible that environmental changes and decadal cycles of atmospheric processes have not left a detectable response in epibenthic community structure in the southern Chukchi Sea during the study period (yet) because many arctic invertebrates are long-lived and integrate temporal variability in environmental conditions on even longer time scales than considered here (Sainte-Marie 1991, Bluhm et al. 1998, Philipp & Abele 2010). Many of the identified taxa also tolerate variability in salinity or temperature (Sabourin & Stickle 1981, Drouin et al. 1985, Charmantier & Charmantier-Daures 1995) as it

occurs seasonally in the southern Chukchi Sea (Woodgate et al. 2005). It is likely that conditions in the southern Chukchi Sea were well within the physiological limits of the local fauna during the study period. Also, the study design only is based on two closely spaced transects rather than a set of transects across the entire Chukchi Sea as implemented in the Distributed Biological Observatory (Grebmeier et al. 2010) and the Arctic Marine Biodiversity Observation Network (AMBON) study that will better allow detection of latitudinal shifts in community structure as recently documented in the Atlantic Arctic inflow area (Fossheim et al. 2015).

4.2.2 Variable abundance and biomass

Some measures of food supply (e.g., infaunal biomass, chlorophyll) correlated to bulk estimates of either abundance and/or biomass in at least one sampling year. No single metric, however, had a temporally consistent relationship with either epibenthic community characteristic over the sampling years. Benthic biomass in polar regions is highly influenced by the supply of food from the overlying water column (Grebmeier & Barry 1991), which in the southern Chukchi Sea shelf is high because of high *in situ* primary productivity (Springer & McRoy 1993, Hirawake et al. 2012) in combination with advective carbon supply from the northern Bering Sea. Typical for most Arctic shelves, pelagic production is tightly coupled with some benthic communities, specifically with high infaunal biomass in some regions (e.g., Grebmeier et al. 2006). Recent studies suggest that primary production has increased 20% in the Arctic (Arrigo & van Dijken 2011) and 41% in the Chukchi Sea (Arrigo & van Dijken 2015) over recent years and epibenthic communities can respond to such changes in food supply. For example, the deep-sea benthic community at the HAUSGARTEN site in the Atlantic Arctic varied in density and structure in response to changes in food supply over a decadal time scale (Meyer et al. 2012). Other deep-sea communities in the North Pacific (Kuhnz et al. 2014) and the Northeast Atlantic (Billett et al. 2001, Wigham et al. 2003) also experienced changes in composition related to variability in food supply over both annual and decadal time scales. In contrast, no consistent relationship was found between measures of food supply and metrics of epibenthic community composition or biomass in the present study (also see Bluhm et al. 2009). The strength of benthic-pelagic coupling with the epibenthic community on the southern Chukchi shelf may be obscured by the mobile predatory/scavenging feeding mode of many of the dominant taxa (Bluhm et al. 2009). Their high mobility allows them to move among patches of high organic matter deposition and they also can exploit multiple food sources, and are thus less directly linked to variability in overlying primary production than more stationary fauna feeding on primary production. In the present study, predators/scavengers dominated the biomass in all sampling years and relative

proportions of feeding types varied little between sampling years. In addition, the strong lateral advection of particles during their sinking (Hwang et al. 2008) can create a mismatch between surface measures of food supply and benthic communities. Alternatively, primary production may not actually have increased in the southern Chukchi Sea over the study period. Disparity exists in temporal trends of primary production between satellite-based regional to pan-Arctic estimates (Arrigo & van Dijken 2015) and regional to sub-regional *in situ* studies that have actually recorded declines in some areas (Lee et al. 2013).

Large temporal differences in the biomass of some taxa over sampling events included the strong increase in arthropod biomass in from 2004 to 2009. This large increase was driven almost entirely by *C. opilio*, which had higher mean body mass per individual in 2009 than 2012, indicating that an abundance of large (adult) individuals contributed to the high biomass in that sampling year. In contrast, snow crab biomass in 2012 was dominated by small individuals (low mean mass per individual), which greatly reduced overall biomass, albeit not abundance, compared with 2009. Such variation may be connected to the life cycle of snow crab. In the eastern Bering Sea, recruitment of large female snow crab occurs cyclically, with cohorts of very large individuals occurring every 6-7 years (Orensanz et al. 2007). This periodicity corresponds well with the average maturation time (7-8 years) of female crabs following egg extrusion (Ernst et al. 2012). Although there is no reported evidence of a similar pattern existing in the Chukchi Sea, these life cycle characteristics could be a possible mechanism for the conspicuous increase in large individuals documented in 2009. The high abundance of small snow crab found in this study in 2012 is indicative of a recent recruitment event (Ruhl 2007). Continuing a longer time series and conducting more frequent sampling (e.g., annual) and obtaining size-frequency data of snow crab would enable a better understanding of snow crab life history on the southern Chukchi shelf.

In addition to variation in snow crab abundance and biomass, a decline in abundance and biomass occurred in the holothurian *Myriotrochus rinkii* from 2004 to 2012, mostly in the southwestern Chukchi Sea. As discussed above, holothurians are able to respond to pulses of fresh detrital material (e.g., Wigham et al. 2003). Holothurians selectively feed on sediment high in organic carbon content and population sizes may be controlled by the amount of plant material available in surface sediments (Ginger et al. 2001, Paltzat et al. 2008). It is possible that the decline of *M. rinkii* populations is linked to lower phytodetritus available in the sediment as evidenced by a simultaneous decline in sediment chlorophyll, which was higher in 2004 than in subsequent sample years. Although a decline in sediment chlorophyll seems counterintuitive at a time with a suggested simultaneous increase in primary

production (Pabi et al. 2008, Arrigo & van Dijken 2011) and in Bering Strait through-flow (Woodgate et al. 2012), increased pelagic grazing and recycling may have reduced vertical particle flux (discussion about such scenarios in Hunt et al. 2002, Carroll & Carroll 2003, Grebmeier 2012). Also, Lee et al.'s (2007) *in situ* measurements of primary production in the region actually suggest declines. Alternatively, or in addition, the distribution of water masses and their particle content could explain the decline in *M. rinkii* in the western Chukchi Sea. In 2004, the extension of the productive AW into the western, coastal regions of the Chukchi Sea water may have supported large populations of *M. rinkii* through the deposition of fresh algal material. Conversely, the cold and fresh Siberian Coastal Current (SCC) periodically brings large amounts of refractory terrestrial material from Russian rivers south into the western Chukchi Sea (Weingartner et al. 1999). The SCC was apparently not present in the southwestern Chukchi in 2004 but was anomalously strong in 2009 (Pisareva et al., in review) and may have been present in 2012. Limited measures of organic content in the sediment and carbon stable isotope values of benthic consumers suggest more assimilated (isotopically lighter) terrestrial material in 2009 and 2012 than in 2004; this would support my hypothesis of a stronger influence of the SCC in 2009 and 2012 relative to 2004. This change in food quality may have affected abundance and biomass of the deposit-feeding *M. rinkii* in the region.

4.3 Spatial and temporal patterns in benthic food web structure

Benthic food web structure can be an indicator of overlying water column processes governing the food supply to the benthic system (Iken et al. 2010). Spatial trends in food web structure over long time scales (years) can, therefore, lend insight about the persistence or variability of these hydrographic processes. Mostly temporally consistent spatial patterns were observed in food web structure of the benthic community, aligning with major water masses in the southern Chukchi Sea. In contrast, such patterns were not detected in the particulate organic matter (POM) food sources in the water column or the sediment.

4.3.1 Patterns in the POM food source

Carbon isotope ratios of POM can be expected to differ among water masses in the southern Chukchi Sea due to variations in the distribution and composition of carbon endmembers, such as different primary producer sources, which are influenced by differences in the photosynthetic pathways (e.g., Peterson & Fry 1987). For example, carbon derived from marine phytoplankton production is typically enriched in ^{13}C compared with terrestrial plant matter due to fractionation that occurs during

photosynthesis (Schubert & Calvert 2001, Wooller et al. 2007). As such, stable carbon isotope distributions of POM in Arctic seas reflect the degree of marine phytoplankton versus terrigenous organic matter influences in the water column (Dunton et al. 2012). Carbon isotope ratios of Arctic marine POM are typically around -23 to -25‰ (Krishnamurthy et al. 2001, Schubert & Calvert 2001, Søreide et al. 2006, Tamelander et al. 2006). These isotope ratios become more depleted in ^{13}C with increased proximity to freshwater sources, which can carry isotopically lighter terrestrial material. Along the Russian coast, for example, rivers carrying terrestrial soil and plant matter (Lobbes et al. 2000) lower the carbon isotope values of POM in the coastal waters of the Kara Sea by about 2‰ compared with offshore POM (Krishnamurthy et al. 2001). Similarly, terrestrial organic matter from the Alaska Rivers and Mackenzie River along the Beaufort Sea coast lowers $\delta^{13}C$ values of POM in the nearshore Beaufort Sea shelf in comparison with the adjacent Chukchi Sea and Amundsen Gulf (Morata et al. 2008, Magen et al. 2010). Accordingly, in the Chukchi Sea, lower $\delta^{13}C$ signatures of POM in coastal water masses (published ranges from -24.8‰ to -22.0‰) have been attributed to a higher proportion of terrigenous organic material when compared with the POM in the BSAW (published ranges -21.0‰ to -23.8‰) that is considered to be derived mostly from autochthonous primary production (Naidu et al. 1993, Khim et al. 2003, Iken et al. 2010).

Similar to carbon stable isotopes, nitrogen isotope values of the POM source may differ with the origin of organic matter based upon differences in isotopic fractionation occurring during nitrogen fixation, assimilation, denitrification in plants or soil microbes, or nitrogen source (Delwiche & Steyn 1970, Sweeney & Kaplan 1980). In 2004, POM $\delta^{15}N$ values in the southern Chukchi Sea differed among water masses, with lower mean $\delta^{15}N$ values in the coastal ACW (4.56 ‰) than the BSAW (5.51 ‰ to 5.63 ‰) (Iken et al. 2010), although the same difference was not observed in the later years of the present study These differences in 2004 may have been in part due to freshwater inflow carrying fresher terrestrial organic matter that is lighter in ^{15}N than marine suspended matter (Middelburg & Nieuwenhuize 1998) into the coastal region. Diagenetic processes, however, can alter nitrogen isotope signatures and obscure source differences (Thornton & McManus 1994).

Nevertheless, given the known differences in stable isotope values for various carbon sources, the spatial POM isotope patterns observed in the study region in 2004 (Iken et al. 2010), and the different productivity regimes between water masses in the Chukchi Sea, it is curious that neither POM isotope marker differed significantly among water masses in this study in 2009 and 2012. This is especially noteworthy as differences in carbon isotope values have been detected over small spatial scales in the

northeastern Chukchi Sea (Tu et al. 2015) and Bering Strait (Iken et al. 2010). As primary producers respond on short time frames (lag time of hours to days; Collos 1986, Landry et al. 2000) to surrounding nutrient and light conditions, the lack of any spatially consistent patterns in POM sources in the present study may hence derive either from high variability in nutrient content in the present study years, from variations in the spatial extent and position of these water masses across years, or from both. Although the concentrations of inorganic nutrients, and subsequently the rates of primary production, may exhibit localized variability (Hill & Cota 2005, Wang et al. 2005), the general differences between characteristics of BSAW and ACW are persistent at the larger regional scale (Hansell et al. 1993, Lee et al. 2014). The location of the spatial boundaries of water masses in the southern Chukchi Sea, however, are variable as a result of wind-forcing (Woodgate et al. 2005) and other factors (Weingartner et al. 2005). In 2009, for example, the extent of ACW reached as far west as Herald Canyon and historical data suggest that this water mass can occasionally occur along the Russian coast (Pisareva et al., in review). Moreover, cross-frontal mixing between BSAW and ACW can occur due to eddies, tides, bottom friction, and wind-induced mixing. Lateral mixing may advect POM from the productive BSAW to the coastal ACW and may be partly responsible for a high degree of spatial and temporal variability in the stable isotope signatures of POM reported here, which may have prevented a detection of possible spatial differences. On the western side of the study area, the SCC was much stronger in 2009 and 2012 than in 2004 (Pisareva et al. in review), suggesting that POM sources in the RC region also were exposed to different hydrographic conditions among study years. Therefore, I suggest that variability of spatial patterns in primary production due to associated variations in water mass mixing and advection likely affected the different patterns in stable isotope signatures of POM found in 2004 versus the later sampling years.

4.3.2 Patterns in benthic food web structure

Food web properties of benthic communities in the southern Chukchi Sea based on $\delta^{13}C$ organism values varied significantly between water masses in all study years. Benthic invertebrates composing the food web assessed here are long-lived and integrate variability over time scales from months to years (e.g., Cabana & Rasmussen 1996, Post 2002). The detectable differences in benthic food web structure among water masses and over study years suggest that the benthic community persistently integrates the temporal variability in water column processes. These differences are likely the result of organisms in BSAW consuming a larger portion of marine derived carbon than those in coastal water. Although some ^{13}C enrichment occurs in benthic organisms during organic matter assimilation (DeNiro & Epstein 1978),

the enrichment is typically small, ranging from 0.8 ‰ to 1.1 ‰ in marine food webs (France & Peters 1997) and possible differences in carbon enrichment among water masses is hence unlikely to account for the differences in food web structure among water masses observed here.

Within water masses, temporal variations in food web structure were observed at the Russian coastal station, likely resulting from differences in carbon sources not detected in the snap-shot POM samples. In 2004, organisms were isotopically enriched in ^{13}C compared with 2009 and 2012 in that water mass. The lower RC organism $\delta^{13}C$ values reported from 2009 coincided with the presence of a strong SCC (Pisareva et al. in review), which may have carried isotopically depleted terrestrial organic matter (Lobbes et al. 2000, Wooller et al. 2007). Although the presence of the SCC has not yet been confirmed for 2012, overall hydrographic conditions similar to 2009 existed in the 2012 sampling year, and POM isotope values between the two years were similar as well. The ^{13}C depleted POM is then assimilated by benthic organisms, which may have caused the lower $\delta^{13}C$ values in benthic taxa in 2009 and 2012. These observations suggest that the RC community is subject to more variable carbon pathways than the other communities.

Benthic food web structure based on nitrogen stable isotope values of organisms also differed among water masses, although only in 2004 (Iken et al. 2010) and 2012. Benthic fauna in BSAW were isotopically depleted in ^{15}N compared with organisms in ACW in both those years. It is possible that long-term differences in organic matter sources between water masses that were not identified in the snap-shot POM samples of this study may account for the isotopic variations of the organisms in these water masses. Should this be the case, it could account for the greater proportion of higher trophic levels among taxa in ACW than in the BSAW food webs: $\delta^{15}N$ of PPOM is the reference point for the assessment of trophic level of consumers, and as no differences in the PPOM $\delta^{15}N$ values between ACW and BSAW were detected, using the measured (low) $\delta^{15}N$ PPOM value in ACW as the food web baseline would have created artificially high trophic level values for benthic consumers. Hence, the differences in food web structure between these two water masses may not reflect true food web differences. This problem could be overcome by using a primary consumer as the reference base for food web calculations, which excludes the high temporal variability of the PPOM source (Cabana & Rasmussen 1996, Vander Zanden & Fetzer 2007). This was done in the food web study of the same area in 2004 and ACW and BSAW food webs were found to be of similar length (Iken et al. 2010).

An alternative or additional explanation for differing benthic food web structure in ACW and BSAW may be a differential presence and utilization of terrestrial organic matter. Terrestrial organic matter is

generally isotopically lighter in $\delta^{15}N$ than marine-derived sources (Middelburg & Nieuwenhuize 1998), but it is a poor food source for marine consumers unless it is microbially degraded (Lefebure et al. 2013, Rontani et al. 2014). The microbial processing of terrestrial organic material into a more bioavailable form constitutes a trophic step in the food web and, thus, renders the resulting organic material food source for benthic consumers enriched in ^{15}N. This process is supported by the temporally consistent gap in nitrogen isotope values between PPOM and benthic consumers in all study years, which was more pronounced in ACW than in BSAW. It is suggested here that this gap may indicate a trophic level step from microbial trophic processing. Thus, with a higher portion of terrestrial matter in the ACW from river import (see discussion above), the larger proportion of taxa and of biomass at higher trophic levels in ACW than in BSAW is likely a result of a larger contribution of the additional trophic level attributed to the microbial loop in ACW.

These findings lend insight towards understanding the dynamics of energy flow in the southern Chukchi Sea. The overall persistent differences in food web structure between ACW and BSAW, despite high variability in the point-measured POM source, may provide a metric by which long-term changes in the trophic dynamics of the Chukchi Sea can be observed. Should there be future permanent changes in the relationships between water masses (e.g., degradation of the differences between ACW and BSAW), shifts in food web structure may occur. As such, the data presented here may provide a benchmark for detecting an ecological response to changing environmental conditions, such as those that may be induced by global climate change.

5. Summary and Conclusion

The present study described the spatial and temporal patterns in epibenthic community and food web structure on the Chukchi Sea shelf in Sept 2009 and 2012, and in comparison with previously published data in the same study region from 2004. Epibenthic communities based on biomass and taxonomic similarities grouped by larger regions (northern versus southern Chukchi shelf) with smaller subgroups within these two regions. The larger geographic groups were shaped by large-scale physical and biological patterns, and smaller subgroupings were influenced by more localized conditions. Some spatial patterns observed here supported well studied patterns in Arctic epibenthic community structure, such as the inverse relationship in dominance between crustaceans and echinoderms (Feder et al. 2005, Ravelo et al. 2014). Temporal patterns described here may provide some insight into the population dynamics of the snow crab *Chionoecetes opilio,* a dominant organism in the southern Chukchi Sea and one of potential socioeconomic importance. Food web structure differed between the coastal ACW and the central BSAW, possibly indicating the integration of long-term hydrographic conditions in the benthic food web, although no differences were detected in POM values between water masses. Consistent with other work from the Chukchi and Beaufort seas (Iken et al. 2010, Dunton et al. 2012, Divine et al.2015), it is suggested here that the microbial processing of terrestrial organic matter in coastal waters accounts for an additional trophic step in the ACW, causing an overall higher proportion of higher trophic level consumers in the coastal water mass. A temporal difference in $\delta^{13}C$ of benthic organisms at the Russian coast seemed to reflect yearly differences in the strength of the SCC, which influences the organic matter source for benthic consumers.

A possible example of documented changes or variability in location of water masses, sea ice cover and attendant biological production regimes (Pisareva et al., in review, Arrigo et al. 2008, NSIDC 2015) may be the progressive decrease in the biomass of the holothurian *Myriotrochus rinkii* in the southwestern Chukchi Sea, concurrent with the variability in the presence of the SCC. While this example may simply represent natural variability, it suggests that dominant species can undergo major shifts in biomass in response to environmental conditions. Similarly, the observed trend that food webs are longer in coastal water masses that are suggested to have a higher proportion of terrestrial material in their POM food source due to an added tropic level from microbial processing, could be used as an indicator of changing conditions in the Chukchi Sea. Should environmental conditions or water masses change more permanently, or should the influx of terrestrial material into the Chukchi Sea increase from increased coastal erosion and melting permafrost input through river systems (Asahara et al. 2012), more

permanent shifts in community composition and food web structure may be expected, and more so in interior than nearshore shelves. Long-term monitoring will be needed to possibly separate natural variability from long term patterns, such as those induced by climate change (Soltwedel et al. 2014). The present study contributes in spatial and temporal coverage to the growing body of recent work being conducted on epibenthic communities (e.g., Bluhm et al. 2009, Blanchard et al. 2013, Konar et al. 2014, Ravelo et al. 2014) and benthic food web structure in the Chukchi Sea (e.g., Iken et al. 2010, Feder et al. 2011, McTigue & Dunton 2014, Tu et al. 2015) to understand the patterns of natural variability and towards a benchmark to assess and predict the impacts of global climate change.

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Appendix

2012

Phylum	Taxa	Feeding Guild	Presence (Stations)	Mean Abundance (Ind. 1000 m^{-2})	Mean Biomass (g ww 1000 m^{-2})
Annelida					
	Arcteobea anticostiensis	Pr	3	245	55
	Brada-like	Unknown	2	226	55
	Brada villosa	De	1	23	148
	Bylgides sarsi	Pr	2	885	840
	Harmothoe imbricata	Pr	2	434	644
	Nephtys caeca	Pr	1	619	1184
	Nephtys punctata	Pr	1	11	34
	Nephtys sp.	Pr	1	6	3
	Pista maculata	De	1	n/a	1216
	Polynoidae sp. 1	Unknown	7	115	66
	Polynoidae sp. 2	Unknown	2	5	4
	Polynoidae sp. 3	Unknown	1	17	3
	Polynoidae sp. 4	Unknown	2	73	15
	Sphinter sp.	Pr	1	6	35
Arthropoda					
	Acanthonotozoma sp.	Unknown	1	19	10
	Amphipoda sp. 1	Unknown	1	2406	144
	Amphipoda sp. 2	Unknown	1	34	2
	Anonyx sp.	Sc	9	229	106
	Argis lar	Pr	9	208	403
	Bathymedon sp.	Pr	1	110	13
	Chionoecetes opilio	Pr	13	2254	4219
	Cirripedia	Su	6	27	3
	Crangon dalli	Pr	4	49	26
	Crangon septemspinosa	Pr	2	21	9
	Eualus gairmardii	Pr	1	229	192
	Eualus gairmardii belcheri	Pr	3	3253	2065
	Eualus macilentus	Pr	1	20	47
	Eualus sp.	Pr	7	2090	1309
	Eualus sp. 1	Pr	3	200	184
	Eualus sp. 2	Pr	3	2435	1419
	Eusirus cuspidatus	Pr	1	19	10
	Hippomedon propinquus	Sc	2	1307	91
	Hyas coarctacus	Pr/Sc	9	258	1008
	Labidochirus splendescens	Sc/Dt/Br	7	23	118
	Lebbeus groenlandicus	Pr	1	36	141

Phylum	Taxa	Feeding Guild	Presence (Stations)	Mean Abundance (Ind. 1000 m^{-2})	Mean Biomass (g ww 1000 m^{-2})
Arthropoda					
	Lebbeus polaris	Pr	1	417	290
	Lembos arcticus	Dt	6	55	20
	Lysianassidae	Pr/Sc	2	129	27
	Melita dentata	Dt	4	114	37
	Monoculodes sp.	Pr	1	432	29
	Neocrangon communis	Pr	6	47	101
	Pagurus capillatus	Sc/Dt/Br	11	141	492
	Pagurus rathbuni	Sc/Dt/Br	7	34	439
	Pagurus sp. 1	Sc/Dt/Br	1	72	506
	Pagurus sp. 2	Sc/Dt/Br	1	18	47
	Pagurus trigonocheirus	Sc/Dt/Br	10	123	579
	Pandalus borealis eous	Pr	1	41	30
	Pandalus goniurus	Pr	7	364	291
	Parampithoe polyacantha	Unknown	1	41	12
	Paroediceros lynceus	Unknown	1	4245	785
	Pontoporeia femorata	De	1	1255	179
	Protomedeia sp., Halirages sp., Ischyrocerus sp.	Su	1	427	19
	Protomedia sp.	Su	1	45	7
	Pycnogonida	Pr	3	4	1
	Rhachotropis aculeata	Pr	3	221	57
	Sabinea septemcarinata	Pr	2	6	4
	Sclerocrangon boreas	Pr/Sc	1	58	216
	Spirontocaris sp.	Pr	9	148	54
	Stegocephalus inflatus	Pr	2	255	105
	Synidothea bicuspida	Br	2	18	6
	Telmessus cheiragonus	Pr	1	4	352
	Weyprechtia pinguis	Unknown	1	19	10
Brachiopoda					
	Brachiopoda	Su	1	7	7
Bryozoa					
	Alcyonidium gelatinosum anderssoni	Su	8	3	424
	Bryozoa sp. 1	Su	4	n/a	3
	Bryozoa sp. 2	Su	1	n/a	6
	Bryozoa sp. 3	Su	2	n/a	5
	Bryozoa sp. 4	Su	1	n/a	3
	Eucratea loricata	Su	7	n/a	23
	Flustra-like, sp. 1	Su	3	n/a	28
	Flustra-like, sp. 2	Su	1	n/a	2

Phylum	Taxa	Feeding Guild	Presence (Stations)	Mean Abundance (Ind. 1000 m^{-2})	Mean Biomass (g ww 1000 m^{-2})
Bryozoa					
	Heteropora	Su	2	n/a	19
Chordata					
	Synascidiacea	Su	1	n/a	1
	Synascidiacea, sp. 1	Su	1	n/a	68
	Ascidiacea sp. 1	Su	1	5	188
	Ascidiacea sp. 2	Su	1	17	6
	Ascidiacea sp. 3	Su	1	48	491
	Boltenia ovifera	Su	1	1	33
	Chelyosoma macleayanum	Su	2	231	852
	Didemnum sp.	Su	1	n/a	6
	Halocynthia aurantium	Su	2	18	56
	Halocynthia japonica	Su	3	8	16
Cnidaria					
	Actiniaria sp. 1	Pr	1	1241	561
	Actiniaria sp. 2	Pr	9	36	1241
	Actiniaria sp. 3	Pr	3	188	1393
	Actiniaria sp. 4	Pr	2	245	2143
	Actiniaria sp. 5	Pr	1	893	4797
	Actiniaria sp. 6	Pr	1	4	4
	Actiniaria sp. 7	Pr	2	556	10186
	Actiniaria sp. 8	Pr	1	4	18
	Actiniaria sp. 9	Pr	2	22	23
	Hydroidea	Su	1	n/a	1
	Hydroidea sp. 1	Su	1	n/a	1
	Hydroidea sp. 2	Su	1	n/a	6
	Hydroidea sp. 3	Su	1	n/a	18
	Hydroidea sp. 4	Su	4	3	3
	Hydroidea sp. 5	Su	1	n/a	6
	Gersemia fructicosa	Su	1	6	35
	Gersemia rubiformis	Su	2	3	5
	Läfoeina maxima	Su	2	2	2
	Stomphia sp.	Pr	3	20	131
Echinodermata					
	Asterias amurensis	Pr/Sc	2	117	466
	Crossaster papposus	Pr	2	11	30
	Ctenodiscus crispatus	De	3	3904	30260
	Gorgonocephalus sp.	Pr	1	41	4295
	Henricia sp.	Pr	1	9	3

Phylum	Taxa	Feeding Guild	Presence (Stations)	Mean Abundance (Ind. 1000 m^{-2})	Mean Biomass (g ww 1000 m^{-2})
Echinodermata					
	Leptasterias arctica	Pr/Sc	4	28	125
	Leptasterias groenlandica	Pr/Sc	9	695	2411
	Leptasterias polaris	Pr/Sc	5	29	1656
	Myriotrochus rinkii	De	2	568	290
	Ophiocten sericeum	De	1	14	7
	Ophiopolis aculeata	Su	2	27	7
	Ophiura sarsii	Pr	3	78	442
	Ophiuroidea sp. 1	Unknown	1	8	1
	Ophiuroidea sp. 2	Unknown	1	12	3
	Ophiuroidea sp. 3	Unknown	4	19	12
	Psolus peronii	Su	2	114	3519
	Stegophiura nodosa	De	6	1086	607
	Strongylocentrotus pallidus	Gr	2	8	476
	Urasterias linckii	Sc/Dt/Br	2	27	2395
Mollusca					
	Admete sp.	Sp	1	26	138
	Admete viridula	Sp	7	119	87
	Amicula vestita	Gr	1	29	58
	Anomalosipho conulus	Pr/Sc	5	39	245
	Beringius sp.	Pr/Sc	1	1	159
	Buccinum angulosum	Pr/Sc	3	6	99
	Buccinum ciliatum	Pr/Sc	1	39	311
	Buccinum elatior	Pr/Sc	2	13	162
	Buccinum polare	Pr/Sc	4	12	347
	Buccinum solenum	Pr/Sc	1	18	54
	Buccinum sp.	Pr/Sc	4	30	448
	Buccinum sp. 2	Pr/Sc	2	362	443
	Chlamys islandica	Su	1	1	66
	Clinocardium ciliatum	Su	1	4	2
	Clinopegma magnum	Pr/Sc	2	3	97
	Crepidula-like	Su	1	3	1
	Cryptonatica affinis	Pr	11	632	3302
	Cylichna alba	Pr	1	926	329
	Gastropoda, indet.	Unknown	3	8	18
	Ischonochiton albus	Gr	1	6	3
	Latisipho hypolispus	Pr/Sc	6	6	60
	Lunatia pallida	Pr	9	88	338
	Margarites beringiensis	Gr	2	29	4

Phylum	Taxa	Feeding Guild	Presence (Stations)	Mean Abundance (Ind. 1000 m^{-2})	Mean Biomass (g ww 1000 m^{-2})
Mollusca					
	Margarites sp.	Gr	5	38	22
	Musculus sp.	Su	1	1	3
	Neoiphinoe coronata	Su	2	12	46
	Neptunea communis	Pr	3	114	962
	Neptunea ventricosa	Pr/Sc	4	12	1455
	Nodulotrophon coronatus	Pr	1	2	13
	Nudibranchia, Coryphella	Pr	1	4	2
	Oenopota harpa	Pr	3	41	37
	Oenopota sp.	Pr	2	46	63
	Onchidiopsis sp.	Pr	2	12	47
	Plicifusus sp. 1	Pr	1	2	20
	Plicifusus sp. 2	Pr	1	2	20
	Pododesmus machrochisma	Su	1	1	17
	Propebela sp.	Pr	2	7	4
	Retifusus sp.	Pr/Sc	1	4	4
	Serripes sp.	Su	7	756	1732
	Solariella sp.	Gr	1	1	1
	Tachyrhynchus erosus	Pr	7	44	60
	Tachyrhynchus spitzbergensis	Pr	2	9	10
	Trichotropis bicarinata	Su	2	2	24
Nemertea					
	Nemertea sp. 1	Unknown	1	164	58
	Nemertea sp. 2	Unknown	4	19	313
Porifera					
	Halichondria-like	Su	1	n/a	46
	Haliclona- like	Su	1	n/a	458
	Porifera sp.1	Su	1	n/a	11
	Porifera sp. 2	Su	1	n/a	46
	Semisuberites sp.	Su	1	n/a	98
Sipuncula					
	Golfingia margaritacea	Dt	1	6	3

2009

Phylum	Taxa	Feeding Guild	Presence (Stations)	Mean Abundance (Ind. 1000 m^{-2})	Mean Biomass (g ww 1000 m^{-2})
Annelida					
	Nephtys sp.	Pr	3	31	31
	Pectinaria granulata	De	2	130	300

Phylum	Taxa	Feeding Guild	Presence (Stations)	Mean Abundance (Ind. 1000 m^{-2})	Mean Biomass (g ww 1000 m^{-2})
Annelida					
	Phyllodoce groenlandica	Pr/Sc	1	57	155
	Polychaeta	Unknown	4	177	91
	Polychaete tubes	Unknown	2	n/a	4708
Arthropoda					
	Amphipod sp. 1	Unknown	1	74	37
	Amphipoda	Unknown	3	1142	272
	Anonyx sp.	Sc	5	686	568
	Argis sp.	Pr	7	95	362
	Chionoecetes opilio	Pr	14	964	19736
	Crangonidae	Pr	3	30	66
	Gammarid sp. 1	Unknown	1	830	1274
	Gammaridae	Unknown	1	21	10
	Hyas coarctatus	Pr/Sc	9	122	791
	Hyppolitidae	Pr	2	508	322
	Labidochirus splendescens	Sc/Dt/Br	7	83	504
	Lebbeus groenlandicus	Pr	1	61	423
	Melita dentata	Dt	2	57	75
	Pagurus capillatus	Sc/Dt/Br	3	413	1015
	Pagurus rathbuni	Sc/Dt/Br	9	404	1404
	Pagurus trigonocheirus	Sc/Dt/Br	4	52	585
	Rachotropis aculeata	Pr	4	294	143
	Sabinea septemcarinata	Pr	5	234	511
	Saduria sabini	Br	4	4760	12513
	Sclerocrangon sp.	Pr	1	158	1767
	Stegocephalus inflatus	Pr	2	74	89
	Synidothea bicuspida	Br	1	2608	2964
	Telmessus cheiragonus	Pr	1	42	1575
Bryozoa					
	Alcyionidium sp.	Su	2	9	61
	Bryozoa	Su	6	n/a	387
	Bryozoa sp. 1	Su	1	n/a	1854
	Bryozoa sp. 2	Su	1	n/a	2299
Chordata					
	Ascidiacea sp. 1	Su	1	3406	35758
	Ascidiacea sp. 2	Su	1	n/a	119
	Ascidiacea sp. 3	Su	3	224	555
	Chelyosoma macleayanum	Su	1	n/a	384
	Styela rustica	Su	1	6	97

Phylum	Taxa	Feeding Guild	Presence (Stations)	Mean Abundance (Ind. 1000 m^{-2})	Mean Biomass (g ww 1000 m^{-2})
Cnidaria					
	Actiniaria	Pr	1	260	3709
	Anemone sp. 1	Unknown	1	216	1129
	Anemone sp. 2	Unknown	3	53	1176
	Anemone sp. 3	Unknown	2	1493	1776
	Anthozoa	Unknown	2	306	2637
	Gersemmia sp.	Su	2	443	784
	Stomphia sp.	Pr	1	43	642
	Urticina sp.	Pr	1	72	2698
Echinodermata					
	Asterias amurensis	Pr/Sc	2	184	4348
	Asteroidea sp. 1	Pr/Sc	1	30	2514
	Crossaster paposus	Pr	3	22	517
	Ctenodiscus crispatus	De	3	7701	23536
	Gorgonocephalus caryi	Pr	1	261	18823
	Henricia sp.	Pr	2	17	19
	Holothurian sp. 1	Unknown	1	42	254
	Holothurian sp. 2	Unknown	2	765	300
	Leptasterias arctica	Pr/Sc	4	146	1056
	Leptasterias groenlandica	Pr/Sc	4	230	1051
	Leptasterias hirsuta	Pr/Sc	6	431	2600
	Leptasterias polaris	Pr/Sc	5	26	3215
	Leptasterias sp.	Pr/Sc	1	96	1998
	Lethasterias nanimensis	Pr/Sc	1	19	280
	Myriotrochus rinckii	De	7	1958	4674
	Ocnus glacialis	Su	2	3550	6618
	Ophiocten sericeum	De	3	5426	21311
	Ophiura sarsii	Pr	8	5438	29982
	Pteraster sp. 1	Pr/Sc	1	8	261
	Pteraster sp. 2	Pr/Sc	1	8	960
	Stegophiura nodosa	De	1	13847	5679
	Strongylocentrotus pallidus	Gr	1	23	853
	Urasterias lincki	Om	1	44	3549
Mollusca					
	Chlamys sp.	Su	1	19	691
	Nudibranchia	Unknown	2	4	167
	Amicula vestita	Gr	1	n/a	113
	Admete viridula	Sp	7	200	148
	Buccinum elatior	Pr	6	40	526

Phylum	Taxa	Feeding Guild	Presence (Stations)	Mean Abundance (Ind. 1000 m^{-2})	Mean Biomass (g ww 1000 m^{-2})
Mollusca					
	Buccinum polare	Pr	7	31	192
	Buccinum angulosum	Pr	1	7	270
	Buccinum sp.	Pr	1	186	1641
	Buccinum solenum	Pr	3	97	739
	Clinocardium ciliatum	Su	1	6	162
	Colus sp.	Pr	8	78	380
	Cryptonatica affinis	Pr	11	1574	6123
	Cylichna alba	Pr	4	1213	354
	Volutopsis norvegicus	Pr	1	1	135
	Trochoidea	Gr	4	1489	757
	Trichotropis carinata	Su	4	37	195
	Ariadnaria borealis	Su	3	121	54
	Neptunea ventricosa	Pr	4	62	2792
	Neptunea communis	Pr	5	111	1551
	Lunatia pallida	Pr	7	337	1072
	Aulacofusus sp.	Pr	3	46	123
	Serripes groenlandicus	Su	3	62	499
	Colus roseus	Pr	2	229	134
	Cylichna occulta	Pr	2	771	437
	Tachyrhynchus sp.	Pr	5	6097	4630
	Propebela nobilis	Pr	4	28	25
	Oenopota sp.	Pr	6	34	37
Nemertea					
	Nemertea	Unknown	2	29	143
Porifera					
	Porifera	Su	1	28	800